CENOCOCCUM FR.

A MONOGRAPHIC STUDY

BY

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Throughout great parts of Europe, in soils of the »mor« type (the raw humus of German terminology) there are frequently found — sometimes on the surface itself, but more often under the carpet of vegetation, or in the upper layers of soil — small hollow black sclerotia, brittle like coal, mostly resembling shot of different sizes. These sclerotia are known in the literature under the FRIES'ian name of *Cenococcum*[1] *geophilum;* but despite the frequency of their occurrence, our knowledge of their nature is very incomplete. In recent mycological works they are little noticed, or even ignored altogether; in handbooks such as ENGLER-PRANTL: Die natürlichen Pflanzenfamilien and RABENHORST: Kryptogamenflora von Deutschland etc. for instance, this species of fungus is not included. It has even been asserted, during the present century, that *Cenococcum* possibly does not belong to the recent fungus flora at all, but should be regarded as sub-fossil; indeed, some doubt has been expressed as to whether *Cenococcum* really is a true fungus.

Under these circumstances, it seemed tempting to make a further study of these mysterious small bodies; and the present work gives the results of our investigations. The work has occupied several years, partly in study of the literature and partly in field and laboratory studies. A preliminary statement was made on the subject by one of the present writers at a meeting of the Danish Botanical Society on the 10. April 1920.

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1) Etymology: κενός empty; κόκκος originally (oak-)gall; also berry, pill.

1. SYNONYMY.

Cenococcum graniforme (Sow.) comb. nov.

Lycoperdon graniforme Sow. 1800. Col. Fig. of Engl. Fungi, Plate 270.

Cenococcum geophilum Fr. 1825. Syst. Orb. Veg. I, Pg. 364.

Sclerotium bomba Dufour, sec. Fr.: Syst. Myc. III, Pg. 228. 1829.

By the courtesy of the Museum authorities at Kew, we have been able to examine an authentic specimen of Sowerby's *Lycoperdon graniforme* and we stated that this species is identical with *Cenococcum geophilum* as indicated by Fries himself. We did not, however, succeed in procuring material from Fries' own collection in *Scleromyc. Suec. exsiccat.* as the specimen in question is lacking both in Copenhagen and Upsala; nor is there, as Professor O. Juel kindly informes us, any other authentic Fries'ian specimen in the Upsala herbarium.

The following exsiccata of *Cenococcum geophilum* have been examined by us and found to be identical with the species mentioned:

Libert: Plantae cryptogamicae quas in Arduenna collegit M. A. Libert 1830—37, nr. 181. [*β. byssisedum*].

Desmazières: Plantes cryptogamiques de la France, ed. II, nr. 1021.

Westendorp & Wallays: Herbier cryptogamique Belge, nr. 79.

Fuckel: Fungi Rhenani, nr. 1072.

Ellis & Everhart: North American Fungi, nr. 942.

Nr. 1912 in Rabenhorst: Fungi Europæi, stated as being *Cenococcum geophilum* Fr. does not contain this species, but is a gall.

2. CENOCOCCUM GRANIFORME IN MYCOLOGICAL LITERATURE.

In the following pages will be found a chronological survey of all references to *Cenococcum graniforme*, or figures of the same, which we have been able to find in extant mycological works. Such works are often difficult to procure, and we have therefore used our best endeavours to render the survey

as complete as possible, giving the necessary quotations; in cases where the fungus has been subjected to closer botanical investigation (SCHMITZ, TULASNE etc.) we have added some critical comments.

J. SOWERBY 1800

It is now 125 years since J. SOWERBY introduced the species into mycological literature under the name of *Lycoperdon graniforme*. The accompanying illustration (Fig. 1) is copied from Pl. 270 in his great illustrated work: Coloured Figures of English Fungi or Mushrooms, 1797—1809, the plate in question being dated May 1, 1800. The text is as follows:

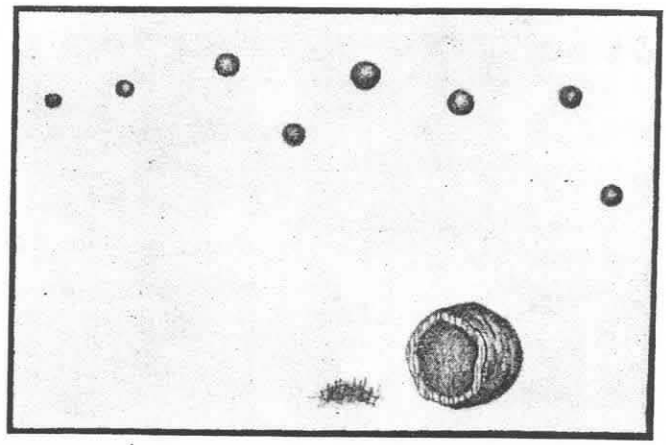

Fig. 1. *Lycoperdon graniforme* SOW. Copy of tracing of Pl. 270 in SOWERBY's »Coloured Figures of English Fungi or Mushrooms« vol. III. 1800. The colouring of the plate is blackish; that of Indian ink.

Tab. CCLXX. Lycoperdon graniforme.

»First shown me in Lord MANSFIELD's wood, Hampstead, by Mr. HUNTER, who showed me the last. It grows loose, lying like small shot above ground without any apparent root. From its first or smallest size it alters but little in colour. The riper ones are very brittle, and crack irregularly. They enclose a black powder.«

E. FRIES 1825—29

The generic term *Cenococcum* was introduced by ELIAS FRIES just a century ago, in his Systema orbis vegetabilis I, 1825, p. 364. FRIES here states that the new genus should take its place in the system between MYLITTA and ANIXIA; for the rest, the fungus is described as follows:

»CENOCOCCUM MOUG. & FR. (Formula: Cbada). Peridium crassum, suberoso-corneum, glabrum, similare, semper clausum, in centro cellula solitaria inani! Obtecta, arrhiza, durissima, atra.

Pyrenium inversum! Duae adsunt species, altera *C. xylophilum*[1]) (olim *Sclerotium*), altera *C. geophilum* (Geophila. P.) a Cel. MOUGEOT missa.

In his catalogue of the plants of Femsiö, Stirpium agri Femsionensis Index, 1825—26, FRIES notes on p. 84 *Cenococcum geophilum*. The parish of Femsiö lies in the western part of Småland. The following footnote is appended to the name *Cenococcum geophilum:*

»Genus omnium diversissimum, vix alii descripto affine. Pilulas Pisi minoris magnitudine, atras, corneas, demum vero intus subpulverulentas cavas sistit species praesens. Frequenter humo mixta praecipue in fagetis, ubi post intensos imbres rivuli pluviales copiose denudant. Sed et alibi vulgare v. c. in humo *Biat. uliginosam* proferente saepius adest.«

It is in the Systema mycologicum III, 1829, p. 65—66 that FRIES gives the first complete description and systematic appreciation of *Cenococcum geophilum*. He ascribes the fungus here to *Trichogastres*, which again is subdivided into *Lycoperdei, Sclerodermei, Podaxidei* and *Cenococcei*. FRIES' description is given here in extenso.

XIII. Cenococcum Fries.

Fries. Syst. Orb. veg. I. p. 364.

»Char. Peridium nudum (haud corticatum), crassum suberoso-corneum, numquam sponte dehiscens, intus primitus similare, dein in sporidia pulverulenta, nullis floccis intertexta, fatiscens et centro cavum. Fungi globulares, arrhizi, sed thallo floccoso passim insidentes.

Morphosis subterranea, difficile observanda, praecipue singularis thallo, qui nunc prorsus nullus, nunc admodum distinctus effusus byssaceus. Peridium jam primitus induratum, pulpa numquam fluxilis observata est. Cetera fere *Elaphomycis*, sed intus prorsus uniforme est, donec in sporidia fatiscit absque

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[1]) This species, which BOUDIER and PATOUILLARD (Bull. Soc. Myc. Fr. XVI: 141. 1900) ascribe to a new genus established by themselves, *Coccobotrys*. evidently does not belong here; it grows on wood, and is clay-coloured outside, white inside. FRIES himself notes that the type of the species differs somewhat from that of *Cenococcum* (Syst. Myc. III, p. 67).

omnibus floccis et cellulis. Os plane nullum, sed vetustissimum fragile evadit et diffractum.

Affinitas et Historia. Omnium hujus ordinis generum distinctissimum, potissimum tamen cum *Elaphomyce* comparandum. Extimum Lycoperdeorum offert radium ad Sclerotaceos, a quibus externa facie subsimilibus sporidiis pulverulentis removetur. Non rara, credo, saltim species primaria, sed ob colorem atrum globuli in humo atra facillime praetervidentur. Nomen a κενος et κοκκος.

1. *C. geophilum,* atrum, sporidiis concoloribus.

Lycoperdon graniforme. *Sowerb. fung. t. 270!* Cenococcum geophilum. *Fries scler. suec. exs. Dec. XXXVII.*

Granula exacte globosa, libera, omni thallo et radice destituta, laevia, glabra, aterrima, magnitudine seminis viciae in humo atra copiosissime nidulantur. Peridium admodum crassum, corneum fere et rigidum, aetate vero fragile fit, contextu obscure vesiculoso; intus demum cavum. Sporidia primo conglobata, compacta. His in terris copiosissimum in humo fagetorum; prima vice attendebam in alveis exsiccatis torrentum novorum, quos aqua largae pluviae tornaverat, in quibus copiose coacervatum, dein multis aliis locis. In ericetis circa Bryères Galliae MOUGEOT!; etiam in crusta *Lecideae uliginosae,* ex Anglia missae, vidi. Autumno. (v. v.)

β. *byssisedum,* peridiis thallo floccoso late effuso atro insidentibus.

Apud nos ne obsoletissimum quidem fili vestigium, cum in hac var. thallus floccocus valde insignis; peridia ceterum prorsus similia. In Gallia circa Angers. GUEPIN! (v. s.)«

In the description here given we encounter for the first time the term spores (sporidia pulverulenta) in *Cenococcum.* We shall have occasion to note, in the following, how this erroneous interpretation of the contents of the *Cenococcum* sclerotium led subsequent authorities astray; the spores once postulated, it must of course be possible to find them, subject them to closer investigation and describe them — and found they were, accordingly, by further erroneous observations, oil globules, or curiously shaped wall fragments being elevated to the rank of spores (vide infra, under SCHMITZ and TULASNE).

FRIES, in his original systematic placing of *Cenococcum* (Syst. orb. veg. p. 364) approximated the genus to *Anixia;* here, however, he includes it among the true Gasteromycetæ on account of the powdery spore mass. This transposition, however, he regrets in the same (third) volume of the Syst. Mycol. in which it is made. For on p. 227, we find, after mention of the *Mylitta* and *Anixia* under *Perisporiaceae,* the following passage:

Cenococcum Fries.

»Obs. Valde invitus hoc genus jam supra inter Trichospermos sive *Gasteromycetes centrales* ob sporidia *demum pulveracea,* quae unicum absolutum characterem inter hos ordines offerunt, inserere coactus fui. Sed etiam in hac evolutionis serie, quam mire continuat, necesse citetur, cum non tantum sporidia primitus intus conglutinata sunt, sed etiam vegetatione prorsus conveniat. Etiam, si habitus solum consulatur, haud facile in alio ordine quaeratur. — — — — Differt a *Mylitta* loculis nullis; ab *Anixia* peridiis demum quidem cavis, sed non dehiscentibus, corneis; — — — — ab omnibus sporidiis demum Lycoperdineorum more, in pulverem liberum solutis. — Synonymis prioribus locis *Cenococco geophilo* adscriptis addendum *Sclerotium bomba.* Dufour!, qui prope Pyrenaeos legit.«

F. G. WALLROTH 1833

In WALLROTH's Flora cryptogamica Germaniæ, Pars posterior p. 264, we find *Cenococcum* included in the group of *Sporomycetes entospori dermatoecii clausi* (together with *Onygena, Pilacre* and *Peridermium).* The genus is called in German Nusssporling, and the species, *C. graniforme,* referred to as follows:

»1803. C. geophilum Fr., sporodochio tornato-globoso libero hypogaeo arhizo atro-piceo fragili viciaeformi, sporidiis compactis foeto, demum inani. — Sub terra laxa fagetorum thuringiac. saepius vidi, quod ignobile plane ac singulare juveni tunc apparuit.«

J. A. WEINMANN 1834 & 1836

A small catalogue of the Gasteromycetæ of Southwest Russia: Enumeratio Gasteromycetum genuinorum hoc usque in imperio ruthenico observatorum (Linnaea IX: 403—16) is of particular interest in this connection, as WEINMANN here,

p. 414, notes no fewer than 4 *Cenococcum* species: *C. geophilum* Fr., *C. phytophilum* Fr. in litt., *C. xylophilum* Fr., and *C. heliophilum* Weinm. Of the three last-mentioned species, *C. xylophilum* has already been mentioned (footnote p. 335); it is undoubtedly generically distinct from *C. graniforme*. The same applies, however, from the description, to the two other species. *C. phytophilum* has a felty-haired, flesh-coloured to rust-coloured peridium, situate on an extended mycelium of the same colour, and is found on the inner side of wooden tubs containing various exotic plants in hothouses. *C. heliophilum* has, it is true, been met with in the open, on black, bare humus soil, but on slopes open to the sun, and the peridium is white-furry.

In his principal work on Russian Hymeno- and Gasteromycetæ, 1836, Weinmann notes *Cenococcum* p. 636.

M. J. Berkeley 1836

Berkeley, in his account of the fungi in Hooker's British Flora (Fungi p. 307) notes *Cenococcum geophilum* Fr. without adding anything of interest beyond what is stated by Fries. As regards localities, this writer mentions only the one given by Sowerby, and the find recorded by Fries, on a *Lecidea uliginosa* crust. Evidently, he has never found the fungus himself.

Th. Nees von Esenbeck & A. Henry 1837

These writers, in their work: Das System der Pilze, I Abt. p. 62 note *Cenococcum geophilum* under the heading of *Gasteromycetes genuini*, without adding anything new to Fries' original description. Some figures of *C. geophilum* β. *byssisedum* are given; they are not particularly good, but undoubtedly represent the form mentioned.

A. C. J. Corda 1839 & 1842

In his well-known work: Icones Fungorum hucusque cognitorum, 1839, p. 17 and Pl. III, Corda gives an excellent description, and some fairly good figures, of *C. geophilum* β. *byssisedum* but strangely enough, he is not acquainted with the principal species. With regard to the ocurrence of the variety, he states that it is found in woods of foliage trees, under rotting leaves, and in dry bogs. Corda's description gives the first anatomical contribution to our knowledge of *Cenococcum* and reveals altogether a correct view of the structure of the sclerotium; we therefore quote it here in extenso:

»Die von SOWERBY t. 270 und von Prof. FRIES als Norm beschriebene Art kenne ich nicht, und wir haben daher die Varietät genauer zu würdigen, welche ein dem *Racodium turfaceum* oder *R. vulgare* ähnliches Wurzelgeflechte bildet und die Grösse eines Mohnkorns bis zu dem eines Senfkorns erreicht. Die Peridien sind klein, kuglig, vollkommen rund und an der Basis etwas eingedrückt, schwarz, fast glänzend, hornartig und sehr hart. An ihrer Aussenfläche entwickelt die Peridie die langen Zellfäden des Myceliums durch Dehnung der Zellen der Peridie, wie man am Querschnitte deutlich sieht.[1]) Diese Fäden sind sehr lang, gebrechlich, braun, durchscheinend und rauhpunktiert, sind einfach, gablig und oft vielfach verästelt, und so zusammengefilzt, dass es fast nie gelingt, auch nur ein kleines Stückchen derselben zu isolieren. Die Peridie ist sehr dick, oft vier bis sechsmal dicker als ihr Hohlraum, und hornartig; sie ist durchaus schwarzbraun, und besteht aus kleinen, dickwandigen, unregelmässig-sechsseitigen Zellen, deren Wände braun und hornartig, dabei spröde und gebrechlich sind. Von aussen nehmen die Zellen nach innen an Grösse zu, und an intensiver Farbe und Dicke der Wande ab, daher sie auch mehr durchsichtig werden. Gegen den Hohlraum zu zerfällt die Peridienwand allmälig in einzelne Zellstreifen, und diese zerfallen noch mehr nach innen in einzelne Zellparthien von höchst unregelmässiger Gestalt, und wir glauben, dass diese Zellparthien, und die einzelnen Zellen die früheren Beobachter für die Sporenmasse und die Sporen selbst gehalten und beschrieben haben. Man sieht jedoch deutlich das unregelmässige Zerfallen dieser Zellen, welche oft in der Mitte reissen, und erkennt, wie einzelne Zellen unmittelbar mit ihren Wänden zusammenhängen, andere aber durch Zwischen-Zellensubstanz und noch andere durch kleinere Zellen verbunden sind. Die Zellen selbst sind von höchst wechselnder Grösse.

So viel nur haben wir an den von uns untersuchten FRIES'schen, LIBERT'schen und an unseren selbst gesammelten Individuen gefunden.«

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1) The figures show, somewhat schematically, that the mycelium threads proceed from the outermost layer of the peridium, but hardly more. CORDA's view is here doubtless the reverse of what is actually the case; the hyphæ in question are not developed from the sclerotium, but have helped to form it.

The exsiccatum (LIBERT, Arduenn. Nr. 181) mentioned by CORDA forms part of his material for investigation; we have ourselves been able to examine this (see p. 365). It certainly does represent the form *β. byssisedum*. The byssus is composed of magnificently granulated hyphæ, with some few smooth ones here and there; the mycelium is often anastomosing and coremium-forming. The interior of the sclerotia is irregularly collapsed with partly torn cells as mentioned by CORDA. The »Zwischen-Zellensubstanz« mentioned by this writer as occasionally connecting the separate cells is nothing but the walls of the paraplectenchyme, seen from the surface. CORDA gives no fewer than 8 figures of the fungus, Figs. 1—4, showing specimens of the sclerotia natural size, and viewed under the magnifying lens, Fig. 5 a section, slightly magnified. Fig. 6, 7 and 8 give microscopic details of the external (Fig. 6) and internal structure (Fig. 7 and 8) of the sclerotium; the two last in particular must be characterised as good.

CORDA's view — which is also correct — that there are no spores in the interior of the *Cenococcum* is further emphasised by the following quotation from his »Anleitung zum Studium der Mykologie«, 1842, p. 137:

»Unmittelbar hieran [viz. *Sphaeriacei*] schliesst sich die Familie der *Sclerotiacei*, an deren unten folgende Gattungen [*Cenococcum* a. o.] noch keine Fruchtorganen aufgefunden werden konnten, daher wir auch gezwungen sind, diese ganze Gruppe als dubiös zu bezeichnen — — — —.«

C. VITTADINI 1843

VITTADINI, the famous authority on subterranean fungi, states (Monographia Lycoperdineorum p. 227) that he has found *Cenococcum* here and there among roots of moss in oak and chestnut woods in the neighbourhood of Milan, both in spring and autumn. We quote the following from his diagnosis of the species:

»Odor debilis. »Sporidia primo conglobata, compacta« FR.«

It will be noted that VITTADINI doubts the existence of spores, and his view is further emphasised by the following (l. c. p. 226):

»Fructificatio hujus generis mihi plane ignota[1])«.

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[1]) In a review of VITTADINI's work above mentioned, L.-R. TULASNE (Ann. Sc. Nat. II. série XIX, 1843, p. 285) writes: M. VITTADINI termine

Nor does he share FRIES' opinion that *Cenococcum* is most nearly related to *Elaphomyces:*

» . . . nec cum *Elaphomycete* certe comparandum, qui tamen vegetationis loco et habitu analogum . . . «

VITTADINI gives illustrations (l. c. Pl. III, Fig. V) of 3 specimens, natural size, and one bisected, slightly magnified; also a higher magnified fragment of tissue from the sclerotium. The figures are not particularly good.

J. SCHMITZ 1843

In Vol. 17 of Linnæa, p. 536—48, Pl. XVIII, J. SCHMITZ publishes a paper »Ueber die Gattung Cenococcum«, which is of considerable interest in several respects, not least as an instance of misconceptions and erroneous conclusions in organogenetics. The paper opens with a description of the occurrence of the fungus (l. c. p. 536):

»Nicht leicht giebt es einen Schwamm, der häufiger auf dem Waldboden anzutreffen und doch mehr übersehen wäre, als die genannte Gattung. Auf und in jeder Hand voll Dammerde, am Grunde von Baumstämmen oder Sträuchern, besonders an Buchen, ist er in grosser Menge und zu jeder Jahreszeit zu finden.«

The writer then, after describing the sclerotia, goes on to speak of »das schwarze, wollige Wesen, das man so oft auf der Oberfläche der Dammerde antrifft« and which he recognises as the mycelium of *Cenococcum*. The earliest stages of development of this fungus, which he had long sought for in vain, were, he believes, found by him in March—April 1843 (l. c. p. 537) in the form of:

»ein weisses, schimmelartiges Wesen, das bald als ein verfilztes Gewebe die Oberfläche überzog, bald als sehr verästelte Fäden sich in der Erde verbreitete, und die feinsten Wurzelfasern auch von lebenden Gewächsen häufig dicht umhüllte, so dass man sie für verdickte Pilzfäden hätte halten können. Verfolgte man diese weissen Schimmelfäden, so fand man dieselben an manchen Stellen verdickt, oder an den Enden allmählig in rundliche oder birnförmige Körperchen übergehend, von denen ich mich durch anatomische Untersuchung und

enfin son travail par la description du *Cenococcum geophilum* FR., dans lequel, moins heureux ou plus véridique que ses devanciers, il avoue n'avoir jamais vu des spores.

Vergleichung der späteren Bildungsstufen mit den früheren überzeugte, dass sie die jungen Sporangien von *Cenococcum geophilum* Fr. waren.«

The white, felty or stringy mycelium referred to, with the roundish or pear-shaped bodies is figured by Schmitz l. c. Fig. A. This figure at once shows that the bodies in question are the initial stages of fruit bodies of an Agaricacea; this is moreover further confirmed by the fact that the writer, on closer investigation of the mycelium, found it was furnished with clamp connections (l. c. p. 538):

»An verschiedenen Stellen — — —, an den Scheidewänden und diesen gegenüber erhebt sich die Oberfläche der Fasern in Wärzchen oder Höckerchen, die sich auf beiden Seiten der Faser als Halbkreise (Fig. D, a. b.), aber von oben gesehen, als kleine Kreischen (Fig. D, c.) darstellen.«

The discovery of clamp connections in the Basidiomycetae is generally attributed to H. Hoffmann[1]), who, in a paper dated 1856 (Die Pollinarien und Spermatien von Agaricus; Bot. Zeit. 1856, p. 137—148 and 153—163) figures and describes these formations in the mycelium of *Agaricus metatus:*

»— — — Zellenfäden, welche theils ziemlich frei ablaufen und nicht selten eine sehr eigenthümliche Form der Septierung zeigen (Tab. V, Fig. 15 i), welche ich bei den verschiedenartigsten Pilzen sehr verbreitet finde, übrigens aber nirgends abgebildet sehe. Ich nenne sie Schnallenzellen nach ihrer Aehnlichkeit — — —.«

Schmitz' figure dated 1843 however (Fig. D, vide our Fig. 2) shows that this writer had, thirteen years prior to Hoffmann, discovered the clamp connections of the Basidiomycetæ — though he was not himself aware of this, being under the impression that he was examining the first developmental stages of *Cenococcum*.

Schmitz, then, regards the small fruit bodies of the Agaricaceae which he accidentally finds in the earth, as the first formation stages of *Cenococcum* sclerotia. In the accompanying reproduction of Schmitz' figures (our Fig. 2), Fig. E presents a longitudinal section through »das junge Peridium« (i. e. incipient fruit-body formation of an Agaricacea) and Fig. H a

[1]) Vide A. Schenk: Handbuch der Botanik. IV, 1890, 386.

longitudinal section through »das reife Peridium« (i. e. *Cenococcum*). SCHMITZ at first finds »nicht die geringste Aehnlichkeit« between the two longitudinal sections, and is beginning to doubt whether they really are different stages of development in the same fungus; on continued investigation however, he arrives at the view that they must be so. The »metamor-

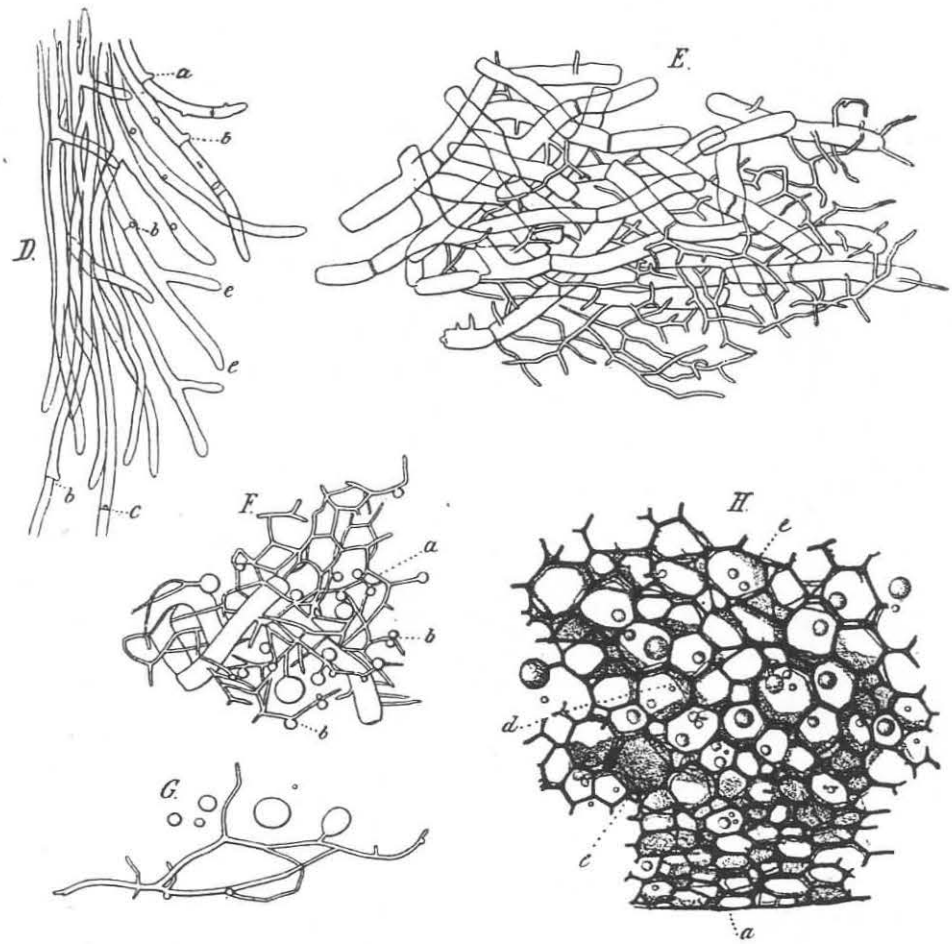

Fig. 2. Copy of Figs. D—H, Pl. XVIII, Linnæa 17, 1843. From SCHMITZ' work: Ueber die Gattung *Cenococcum;* see Text.

phosis« is supposed to be shown in Figs. E, F and H (see our Fig. 2). Figs. E and F probably represent in reality sections of young fruit bodies of a *Russula* or *Lactarius* species, whose tissue is composed in just this fashion, partly of thin, partly of bladder-shaped hyphæ (SCHMITZ' »Fasern« and »Schlauchzellen«). SCHMITZ' conception of the transition from this loose Agaricacea structure to the massive paraplectenchyme of the *Cenococcum* sclerotium will be seen from the following passage (l. c. p. 542):

»Rings um [die Schlauchzellen] — — so wie an ihren Enden, entspringen höchst feine, durchsichtige, ungegliederte, aber ästige Fasern, wodurch nicht bloss eine seitliche Verbindung der [Schlauchzellen] unter einander, sondern auch die von sonst getrennten Enden vermittelt wird (Fig. E) — — —. Dadurch nun, dass die unter einander selbst verästelten Fasern sich rings um [die Schlauchzellen] legen, und sie so zu sagen umstricken, bildet sich auf ihnen ein 4- bis 5- bis 6-maschiges Fasernetz, dass besonders in einem spätern Zustande der Peridien, da die Faser allmählich dunkler werden, deutlich hervortritt (Fig. F). Daher erkennt man auf den Schnitten von älteren Peridien auf den ersten Blick nur dass Fasernetz, bei genauerer Betrachtung lassen sich aber immer noch die darunter befindlichen [Schlauchzellen] — — — — wahrnehmen (Fig. H).«

In other words, SCHMITZ regards the paraplectenchyme of the *Cenococcum* sclerotium as a network of thin hyphæ enveloping a system of bladder-like cells — an error already evident to TULASNE[1]).

To this erroneous interpretation of the structure of the sclerotium, due to faulty organogenetic premises, SCHMITZ now adds a further error in the description of the *Cenococcum* »spores« (l. c. p. 546):

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[1]) TULASNE: Fungi Hypogaei, p. 180—181: »Il nous paraît extrêmement probable que M. SCHMITZ s'est mépris au sujet de ce curieux champignon, et que les jeunes individus parfaitement blancs dont il a fait l'analyse appartenaient à une toute autre plante, puisqu'en effet, d'après ses propres descriptions et ses dessins, on ne peut méconnaître les nombreuses dissemblances qui existent entre la structure de ces prétendus *Cenococcum* jeunes et celle des véritables *Cenococcum* qu'il a étudiés dans leur maturité. Tous les *Cenococcum geophilum* que nous avons observés et parmi ceux il s'en est souvent rencontré de manifestement jeunes encore, — — — étaient uniformément noirs ou d'un brun noir, de même que les *Elaphomyces* et les Truffes noires, si jeunes qu'ils soient, ont à peu près la coloration qu'ils présentent à l'état adulte. Nous ne croyons pas davantage que le *mycelium* du *C. geophilum* soit d'abord blanc, et ne se développe pas tout d'abord avec sa teinte brune.

A l'égard de la structure des soi-disant *Cenococcum* jeunes observés par M. SCHMITZ, quelques efforts qu'il ait faits pour la concilier avec celle des vrais *Cenococcum*, nous ne saurions considérer avec lui ces structures comme indiquant seulement des époques différentes dans le développement d'une même espèce végétale.«

»Was die Sporen anbetrifft, so ist aus der ungeheuren Menge, welche auf einem Schnitte frei herumschwimmt, zu schliessen, dass sie in gedrängter Anzahl die Netzfasern besetzen, wie schon auf Fig. F. und H. [our Fig. 2] hervorgeht, aber durch das Instrument gewaltsam abgerissen werden. Wie schon aber angegeben, erscheinen sie in den mannigfachsten Grössen, sind aber stets von kugelförmiger Gestalt, milch- oder bläulich-weiss, halb durchsichtig, und von einer im Wasser wenigstens weichen, gerinnbaren Substanz, so dass sie bei der Berührung manchmal in einander fliessen. Die schwarze russartige Farbe der reifen Sporangien rührt also wahrscheinlich nicht von der Sporenmasse, sondern hauptsächlich von den schwarzen Netzfasern und den dunklen Membranen der Schlauchzellen her.«

It is evident from this description that the supposed spores are nothing but the oil globules with which the *Cenococcum* sclerotium is at certain seasons of the year filled to such a degree that when crushed in water it turns the water white with a milky emulsion [1]).

SCHMITZ concludes his paper with a generic diagnosis adapted to his results, and consequently erroneous (l. c. p. 548):

Character gen. Cenococci.

»Peridium nudum (haud corticatum), primitus e floccis mycelii ortum, carnosum, tum crassum, suberoso-corneum, fragile, in centro laxiore cavum, intus spurie cellulosum, numquam sponte dehiscens, sed dein fatiscens. Sporidia globosa capillitio reticulato fibrarum articula subcylindrica obtegenti insidentia. Fungi globulares, atri, mycelii fibris byssaceis nigris adnexi.«

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[1]) TULASNE: Fungi Hypogaei, p. 181: »Les corps que le même auteur [M. SCHMITZ] regarde comme les spores du *C. geophilum* ne sont, il faut le reconnaître, que de simples gouttes d'huile qui sont abondamment répandues dans le tissu cellulaire constitutif du *peridium;* nous avons peine à comprendre que le savant Allemand se soit mépris à ce point, lorsqu'il a lui-même observé que ces prétendues spores étaient fort inégales en volume, et que, rapprochées entre elles, elles s'associaient les unes aux autres — — — —. M. SCHMITZ fait naître ces spores à l'extrémité de certains filaments associés en réseau, mais les adhérences qu'il signale sont évidemment toutes fortuites et n'impliquent aucun rapport organique, ce dont nous nous sommes d'ailleurs assurés.«

El. Fries 1849 — E. Fries, in his Summa Veg. Scand. II, p. 445, gives a diagnosis of *Cenococcum* which is in all essentials an excerpt from that of Schmitz.

G. W. Bischoff 1860 — Bischoff, in his Handbuch der botanischen Terminologie und Systemkunde, II Abt., Pl. 74, Fig. 3685, gives a rather bad figure of *Cenococcum geophilum β byssisedum*.

M. J. Berkeley 1860 — M. J. Berkeley, in his Outlines of British Fungology p. 304, gives *C. geophilum Fr.* with the observation that the systematic position of the species is very uncertain. He is now (cf. p. 338) evidently acquainted with the fungus, which is stated as being common on peaty soil in woods.

L.-R. & C. Tulasne 1862 — In the handsome and important folio work: Fungi hypogæi, in which the brothers Tulasne have described and figured in masterly fashion the subterranean fungi known at that time, mention is made on p. 179 - 81 (see also Pl. XXI, Fig. VIII) of *Cenococcum*. In regard to the generic description the following new characters should be noted, with which Tulasne[1]) supplements the knowledge of botanists of the period regarding this fungus (l. c. p. 179):

»Guttulae oleosae in peridii contextu creberrimae, in gleba multo rariores vel nullae. Sporae minutae globosae subsphæricae nigrescentes et subopacae; episporio levi aut aliquando (ni fallimur) veluti reticulato.«

The writer then quotes Schmitz' generic diagnosis, which he considers »fortassis non extra errorem«. As regards the systematic position of the fungus, Tulasne states:

»Cenococcum sibi natura affines nondum clare prodidit; habitu et crescendi modo ad *Tuberaceos* et potius forsan ad *Elaphomyceos* accedit, sed structura interna ab eis facile discriminatur. Illius fructificatio quae plurimis mycologis penitus latuit, pro rite nota etiam nunc haberi nequit.«

On p. 180 there follows a detailed description of the species, in Latin, and a list of localities noted by previous writers as well as those discovered by the authors of the work in question. The following will be of interest here:

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[1]) The principal author of the work is L.-R. Tulasne.

»Vitri sufficienter augentis ope examinatae, ambae regiones [i. e: interior et exterior] utriculis polygonis globosis subaequalibus arcte coalitis et plerumque prorsus vacuis conflantur, quibus parietes crassi caesio-vel fuligineo-nigri. Utriculi magis excentrici, sive peridii proprii, guttulis oleosis pallidis crassis frequenter pro parte replentur, interiores ut plurimum eisdem destituuntur. *Sporae* quarum hactenus originem eruere seu primordia in suffulcris aut conceptaculis propriis videre non licuit, in glebae penetralibus degunt globosae, subsphaericae nigrae aut fuscae, subopacae, leves (immaturae ?) aut aliquando (maturae ?) reticulo paulo irregulari et marginem angustum praestante in superficie notatae. *Odor* nullus, vel non peculiaris. — — — — In castanetis et ericetis agri Parisiensis fere ubique, ac quovis anni tempore abundantissime reperitur. In locis similibus Pictaviae — — a. cl. S. DE LACROIX effossus est.«

The specific diagnosis is followed by a detailed discussion; two passages of which we are already acquainted with, namely those criticising the work of SCHMITZ (see footnotes p. 344—45). With regard to the occurrence and manner of growth of the fungus we read:

»Quoique ce petit champignon soit extrêmement commun dans les bois des environs de Paris, il ne nous est pas souvent arrivé de le rencontrer vivant, ou du moins encore attaché au *mycelium* brun noirâtre au milieu duquel nous pensons qu'il se développe toujours. Nous avons vu plusieurs fois ce *mycelium* envahir des touffes de *Dicranum glaucum* languissantes, et donner naissance à *Cenococcum* au milieu des feuilles et jusque vers le sommet des tiges de cette mousse. Le jeune champignon adhère à son *thallus* nourricier par un grand nombre de points; il en est complètement révêtu, mais en mûrissant il se dépouille de cette enveloppe, devient lisse et persiste en cet état dans le sol pendant fort longtemps. Nous l'avons toujour vu brun-foncé ou noir — — —«.

As will be seen from the above generic diagnosis compared with the footnote p. 345, TULASNE shows that SCHMITZ' »spores« are only oil globules. And though the »spores« which TULASNE offers us in exchange will not bear the test of closer investigation, it is nevertheless to the credit of this able mycologist that he should have succeeded, with the optical aids available in his day in discovering the »spores« at all and

giving a good description of their appearance; for these bodies, which form a very characteristic component in the interior of the older *Cenococcum* sclerotium, are often only 3–5 μ in diameter (»environ 7.5 μ dans leur plus grand diamètre«. TULASNE).

The accompanying Fig. 3 is a copy of that given by TULASNE for *Cenococcum*; it represents part of a transverse section of the sclerotium, with the scattered »spores« in the cells, s, and some oil globules, g. We will not here enter into any interpretation of Tulasne's spores, which will be considered in a later chapter (see p. 370) but will merely note that these so-called spores are in reality wall fragments, with a fairly regular, roundish outline.

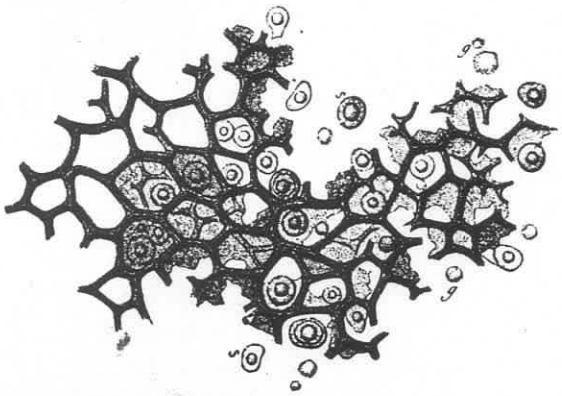

Fig. 3. Copy of Fig. VIII Tab. XXI in TULASNE's Fungi hypogæi. 1862. The figure represents part of a section through the *Cenococcum* sclerotium; g: oil globules, s: »spores«.

L. FUCKEL 1869

FUCKEL, in his Symbolæ Mycologicæ, p. 248, records *Cenococcum* under *Elaphomycei* but makes only brief mention of the species:

»Ich sah bis jetzt weder Schläuche noch Sporen. — Auf und in feuchter Haideerde, selten, im Herbst. Im Oestricher Wald an mehreren Stellen.«

M. C. COOKE 1871

Cenococcum is noted in the Handbook of British Fungi p. 371, with references to literature and exsiccata. The description is altogether a repetition of that given by BERKELEY, with additions from TULASNE. Fig. 118 reproduces NEES VON ESENBECK's picture of the fungus, the plate, unfortunately, being reversed.

E. ROSTRUP 1884

At a Meeting of the Danish Botanical Society in Copenhagen on the 24. April 1884, E. ROSTRUP made a statement as to subterranean fungi in Denmark, from which the following passage may be quoted (Medd. fra Den Bot. Foren. i København I, S. 104):

»In October 1878 I received from Dr. P. E. MÜLLER a quan-

tity of heath soil for investigation with regard to mycelium of fungi in the same. In one of these samples, from low oak scrub near Herning, I found several specimens of *Cenococcum geophilum* FR. a species not previously known in Denmark. These were blackish-brown fruit bodies, big as a vetch-seed, hard like coal, with blackish spherical spores; the species is ascribed by TULASNE to a special group of the *Tuberaceæ*.«

In the Index to SCHROETER's: Die Pilze Schlesiens we may look in vain for the name *Cenococcum*. The fungus is, however, mentioned in the introductory survey p. 69: C. SCHROETER 1889

»Auch *C. geophilum* . . . . . Pilzkörper, bei denen noch keine Fructification bekannt ist, dürfte wohl ein sclerotiumartiges Gebilde sein.«

In American literature, *Cenococcum* seems to be very little noted. Dr. C. L. SHEAR, of Washington D. C. has kindly furnished the present writers with the following statement, in a letter dated May 1916: J. B. ELLIS 1889

»I have looked up the question of the occurrence of *Cenococcum* in America and find that but one collection so far has been reported. It is mentioned by ELLIS in BRITTON's: Catalogue of Plants found in New Jersey, 1889, Pg. 601, as found »in cultivated soil.« Specimens apparently of this collection were distributed by ELLIS & EVERHART in their Exsiccati Nr. 942, Newfield, New Jersey, June. — — — I am enclosing a few fragments. — — — —«

The Sylloge Fungorum gives, in Vol. VIII, p. 871, a brief description of *Cenococcum*, with literature references, and in Vol. XIX, p. 238, a list of extant illustrations. P. A. SACCARDO 1889 & 1910

A more comprehensive mention of *Cenococcum* is given by TH. FRIES in his work on Scandinavian truffles and tuberaceous fungi, p. 266 - 268 (Swedish). The genus is diagnosed as follows: TH. M. FRIES 1909

»Fruit bodies subterranean, hollow inside; *gleba* formed of polygonal closely united cells (spore sacks?); the spores, which are liberated on decay of the cell walls, are almost spherical.«

With regard to the occurrence of the species, we find inter alia:

»*Cenococcum* hardly appears to have been observed in a living state in Sweden during the past 70 - 75 years, but the species is perhaps not rare in the south of Sweden, especially Scania and the west of Småland (Femsiö: E. FRIES). It was also included in FRIES' Summa Veg. Scand. II, locality not stated, for Svealand. — How far it may also have been found in Denmark in a living state is perhaps uncertain; this was perhaps the case with the specimens found by E. ROSTRUP in a common spruce wood in the Stendalgaard Plantation. . . . On the other hand, it is found (in Sweden) abundantly in a subfossil state, showing that it must have been widely distributed in earlier times and occurred in great abundance. . . . . The same is perhaps the case as regards Denmark, though it has hitherto only been recorded from a very few localities there.[1])«

J. LIND 1913

J. LIND, in his list of fungi in ROSTRUP'S Herbarium (Danish Fungi as represented in the Herbarium of E. ROSTRUP) states p. 153 that he has found *Cenococcum* by the thousand both in Calluneta and Querceta in Jutland; and further:

»It will no doubt be found everywhere where moor-formation occurs in the soil of forests; its presence has been noted in the sandy parts of Jutland and Sealand, both under *Picea, Fagus, Quercus* and *Calluna*. . . . .«

If the writer had confined his observations on the fungus in question to its ecology, it would have been well enough; unfortunately, however, he allows himself to indulge in some remarks of a mycological character which were better omitted:

». . . only very seldom have I found them *(Cenococcum)* to be divided into chambers inside such as delineated by TULASNE (Hypogaei). . . . .«

»It is to be doubted if the small, hollow, black, brittle

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[1]) With regard to one of the Danish localities, O. GALLØE states, according to a letter: »It occurs here in numerous sizes from 2 - 3 mm to abt. $^1/_2$ cm., i. e. varying considerably as to size, but always hollow inside. I have found it everywhere in beech mor, closely embedded in the peaty mass of the mor. I have found it right up to the surface of the mor, only hidden by an inconsiderable covering of leaves, and it seems to me therefore less likely that it should be subfossil; it lives here doubtless to this day«.

balls are true fungi; TH. FRIES considers them to be dead and subfossile remnants of a fungus; others even consider them only a conglutination of humous matters which for unknown reasons assume this shape. — — —«

The literary documents which we have brought forward in the foregoing show very distinctly that only the earlier writers have made any serious attempt to elucidate the true nature of *Cenococcum*. The culmination is reached by TULASNE in 1862. Later writers have not concerned themselves with anatomical investigation of the fungus, and offer nothing new beyond contributions to its ecology; and here too their ideas gradually become uncertain and erroneous. It seems as if the fungus has been »given up« by the botanists; the great systematic works omit it from their indices; neither RABENHORST nor ENGLER-PRANTL mention *Cenococcum graniforme*, and by way of example, there is no mention of it in such a work as P. MAGNUS' Die Pilze von Tirol, 1905, though this gives over 3500 species of fungi. In contrast to this, *Cenococcum* has become a frequent occurrence in modern palæontology, as we shall have occasion to note in the following section.

3. CENOCOCCUM GRANIFORME IN PALÆONTOLOGICAL LITERATURE.

Cenococcum graniforme is a fossil of frequent occurrence in fresh water deposits of widely different character, from the pleistocene to the subrecent; and the species is accordingly often mentioned in works on palæontology. We give here the most important references in this connection.

The first palæontologist to draw attention to the fossil occurrence of *Cenococcum* seems to have been C. A. WEBER. In a letter dated April 1916, this writer kindly informed us as follows: C. A. WEBER 1896, 1904 & 1914

»Ich fand *Cenococcum geophilum* FR. zuerst in interglazialen Ablagerungen Schleswig-Holsteins, konnte es aber erst bestimmen, nachdem ich es lebend angetroffen hatte. Meines Erinnerns wurde es von mir zum ersten Male öffentlich er-

wähnt in einer Abhandlung: Über die fossile Flora von Honerdingen u. s. w. (Abh. Naturw. Vereins zu Bremen, 1896, XIII: 436). Die Fruchtkörper fanden sich dort in diluvialem Süsswasserkalk eingeschwemmt vor. Seitdem ist sie mir überaus häufig in interglazialen wie glazialen und in alluvialen Ablagerungen Nord- und Mitteldeutschlands begegnet. Sie findet sich besonders häufig, ja fast regelmässig in sandigen Wald- und Heidetorfschichten am Grunde der Moore vor. Die ältesten mir bisher bekannten Vorkommen dürften der Mammutschicht von Borna südlich von Leipzig (Abh. Naturw. Ver. Bremen 1914, XXIII) und das praeglaziale Torflager von Lüneburg (Abh. d. Kgl. Preuss. Geol. Landesanstalt, Neue Folge Heft 40, 1904) sein, das vielleicht als spätpliocen zu bezeichnen ist.«

Gunnar Andersson 1898, 1902 & (1909)

Gunnar Andersson, in his: Studier öfver Finlands Torfmossar och fossila Kvartärflora (Studies in the Peat Bogs and fossil quaternary flora of Finland) 1898, p. 139 - 40; Pl. II, Figs. 165 - 71, describes and delineates subfossil *Cenococcum*. We may here quote the following:

»The systematic position of the fungus is, as far as I have been able to ascertain up to now, almost unknown. Frank (Leunis Synopsis der Pflanzenkunde, 3. Ed. 1886, vol. 3, p. 370) says the same, and places it somewhere near *Elaphomyces*. Despite kind assistance from Prof. Lagerheim, it has not yet been possible to determine what part of the fungus these small granules really represent. He has however pointed out that they may perhaps be closely related to the *Sclerotium hydrophilum* Sacc. described in detail by Rothert (Bot. Zeit 1892). — Undoubtedly identical with *Cenococcum geophilum* are, as first pointed out by C. Weber, some small black formations known for many years past from the bogs of Sweden; this identification however, only gives us a name, and adds nothing to our knowledge of the fossil. It varies very considerably in size (Pl. II, Figs. 165 - 71). Under the microscope, these fossil bodies reveal a fairly large-celled, radially arranged tissue. In the Dryas zone, only an extremely small form of the fossil, a mere speck, has been observed. *Cenococcum* is extremely frequent in alder and other peat containing roots of trees in large quantities.«

The writer then mentions 3 fossil occurrences from Finland, and adds that the distribution of the fungus in that country is entirely unknown to him. — In GUNNAR ANDERSSON'S work: Hasseln i Sverige (The Hazel in Sweden) several finds of *Cenococcum* are recorded, and the writer has also since informed TH. M. FRIES (TH. FRIES l. c. p. 267) that he has found *Cenococcum* in Sweden in peat strata of very dissimilar ages at more than 100 localities ranging from Scania in the south to Lapland, »mostly in such kinds of peat as may be supposed to have been formed of low moors or old forest soil etc. but extremely rarely in those formed of deeper water«.

The writers mentioned give *Cenococcum* (Danske Diatomé-jord-Aflejringer — Deposits of Danish Diatom-earth — p. 17) as found in diatom-earth together with *Taxus, Picea, Pinus, Carpinus* etc., i. e. in strata of interglacial age. N. HARTZ & E. ØSTRUP 1899

HOLMBOE shows, in: Planterester i norske torvmyrer (Vegetable Remains in Norwegian Peat Bogs) that *Cenococcum* is a generally distributed fossil in Norway. He writes, l. c. p 112: J. HOLMBOE 1903 & (1909)

»They [*Cenococcum*] are chiefly found in alder peat, but also in bog peat and most of the other soils deposited in open water. The size of the balls varies from 0.5 - 3.5 mm. . . . . In Sweden and Finland also this fungus is very common as a fossil. It is not known in a living state in Norway.«

HOLMBOE further states, in a letter to TH. M. FRIES (TH. M. FRIES l. c. p 268) as follows:

»It [*Cenococcum*] is found everywhere, extremely common in peat bogs, especially such soils as are formed in open water, most of all perhaps in alder peat. I have found it throughout the whole country from Smaalenene and Lister right up to Risøen in the province of Tromsø; in the inland districts of the eastern frontier as well as out on the sea coast, e. g. at Jæderen and near Bergen. It is found already in the deposits of the birch zone, (i. e. early *Ancylus* period) and I have also frequently found it in quite new, subrecent deposits. I have not hitherto met with it in a living state, but have, it is true, never looked for it.

The fungus is found sometimes in sand and clay strata, sometimes in fresh water chalk and gytje, sometimes again

in peat and peat mud of different sorts (Sphagnum peat, *Carex* peat and alder peat). The most frequently occurring woody plants with which *Cenococcum* is found associated are *Betula alba, Pinus silvestris,* and *Alnus glutinosa.* In several places also we find *Picea* or *Quercus,* and in one or two localities *Betula nana.* Heath plants such as *Empetrum nigrum* and *Calluna* occur here and there.«

L. v. Post 1906

v. Post records, in his Norrländska Torfmossastudier (Studies of the Peat Bogs of Norrland in Sweden) numerous localities for *Cenococcum* from postglacial peat bogs in Norrland. The northernmost find would seem to be that at Arvidsjaur in the Pite Lappmark. This writer finds the fungus here and there in mud and gytje with birch twigs; it is found most frequently however, and most abundantly, in those strata of the bogs where the peat is rich in stumps, or at least fragments and twigs of birch and fir *(Pinus silvestris).* On p. 211 for instance, we find mention of a stratum with tree stumps under sphagnum peat, with numerous rooted stumps of *Pinus silvestris.* On washing 250 cm^3 of the mould peat from this horizon no fewer than 216 fruit bodies of *Cenococcum* were found, varying in size from 0.5 to 2 mm.

N. Hartz 1909

N. Hartz, in a comprehensive study: Bidrag til Danmarks tertiære og diluviale Flora (Contributions to the tertiary and diluvial flora of Denmark) with a summary in English, describes the fossil flora of Denmark's tertiary, pre-glacial and interglacial fresh water deposits. A casual glance at the writer's tabular surveys at once shows that *Cenococcum* is among the most common of all fossils found. We shall in the following excerpt consider the pre-glacial and interglacial periods separately.

1. Pre-glacial deposits. The so-called amber-pin beds, l. c. p. 91, are embedded as dark strata in the fluvio-glacial sand, and contain a mixture of tertiary and quaternary vegetable remains. The amber-pin beds are situated on a secondary bed; their age cannot be determined precisely, but they must be considered as pre-glacial (pleistocene), and are the oldest plant-bearing deposits in the diluvium of Denmark. L. c. p. 119 there is a table showing the plant fossils found in

the amber-pin beds, from which it appears that *Cenococcum* is found in 9 out of the 12 localities investigated (6 in the vicinity of Copenhagen, one on the island of Hveen, one at Bovbjerg and one at Itzehoe). The sclerotia are found among vegetable residue, partly tertiary (stumps of wood and seeds of *Brasenia purpurea),* partly diluvial *(Taxus, Pinus silvestris, Carpinus, Corylus* etc.).

Certain fossiliferous gytje and clay deposits on primary beds must also be designated as pre-glacial. On p. 133 of the work quoted there is a list of the plant fossils found in the lower moraine in Copenhagen Free Harbour, and on p. 135 a list of plant remnants from the *Corbicula* bed at Førslevgaard (Sealand). In the former of these deposits *Cenococcum* occurs embedded in a mixture of tertiary and quaternary plant residue, (tertiary wood fragments and among diluvial species *Taxus, Picea, Corylus* and *Limnanthemum nymphæoides* etc.); in the *Corbicula* stratum on the other hand, where only a single *Cenococcum* hardly 1 mm in diameter was found, there were only diluvial species.

2. Interglacial deposits. Bogs and other fresh water deposits from the interglacial period are widely distributed in Denmark, especially in Jutland. On p. 257—65 l. c. there is a table showing all remains of animals and plants from the interglacial deposits investigated, comprising 16 localities in all, of which 13 are in Jutland. *Cenococcum* is found at ten of these localities, all situate in Jutland.

The following survey of the wood-plant flora of these deposits will show that *Cenococcum* is found partly in »warm« partly in »cold« horizons; the strata in question may be described, now as old diluvial land surface (forest, tundra) now as twig peat, *Sphagnum* peat or transition strata, or again as gytje, clay or sand. The remains of wood plants found in the »*Cenococcum* strata« show very distinctly that the ecological conditions during the period of deposition were widely dissimilar. The following principal types of plant communities may be distinguished:

1. Taxus, Ilex, Tilia grandifolia.

2. Taxus, Picea, Alnus glutinosa, Betula odorata, Fraxinus [Corylus, Carpinus, Quercus].

3. Pinus silvestris, Betula odorata, Calluna, Empetrum nigrum.

4. Betula subalpina, B. nana, Calluna, [Vaccinium uliginosum].

5. Betula nana, Arctostaptylos alpina.

6. Dryas octopetala, Salix polaris.

Cenococcum must thus in those distant ages have grown under highly varying ecological conditions; now in arctic or subarctic formations (Tundra, heath, scrub), now in temperate formations (heaths, heath moors, woods). The size of the sclerotia varies greatly; by way of example we may note that in formation No. 1 (Brørup, *Sphagnum* peat) they varied from 2 - 3.5 mm, while in formation No. 4 (the same bog, fresh water sand at bottom of bog) they were very small, 0.3 - 0.5 mm diameter. This confirms the observations of others to the effect that under cold and poor conditions, the sclerotia become small, or rather small.

K. JESSEN 1920

A natural continuation of HARTZ' work is furnished by JESSEN's: Moseundersøgelser i det nordøstlige Sjælland (Bog Investigations in North-eastern Sealand) which deals solely with late-glacial and post-glacial fresh water deposits. The writer has found *Cenococcum* in the following deposits (Table l. c. p. 178):

Period	Climate	Trees and bushes immigrated during the Period
Beech period (Present)	Present	
Mixed Oak wood period	Warm, first moist later dry	*Carpinus, Fagus*
(Fir period)		
Younger Dryas period	Arctic-subarctic	*Dryas octopetala, Arctostaphylos alpina, Betula nana,* arctic willows
Allerød period	Temperate continental climate	*Betula nana, intermedia, pubescens, Juniperus communis, Pinus silvestris, Populus tremula* etc.
(Earlier Dryas period)		

In strata from the earlier Dryas period, which is prior to the Allerød period, and in strata from the fir period, which follows the younger Dryas period, the writer has not come upon *Cenococcum* in his investigations.

The fossil *Cenococcum* is so characteristic that the records of its occurrence in extant palæontological literature may doubtless be taken as correct in all cases; it is hardly possible to make any mistake here. We have had opportunities of examining fossil *Cenococcum* from two localities (coll. N. HARTZ) both interglacial (HERNING) and sub-recent (»beech layer« in Vendsyssel). Both were, in point of habitus and microscopically, entirely alike, and resembled in all essentials dry, recent sclerotia, having, for instance, distinct TULASNEAN spores; the colour of the paraplectenchyme wall (surface view) was however, in the fossil specimens, a shade deeper reddish brown than in the living specimens.

4. GEOGRAPHY.

From fossil and recent finds of *Cenococcum graniforme,* it may be assumed that the fungus is to this day generally distributed on ecologically suitable sites in the arctic and temperate zones of the northern hemisphere. Future investigations as to the geographical distribution of *Cenococcum* will doubtless confirm this view, and show that the localities noted in the following are only to be regarded as samples of the occurrence of the fungus within its area of distribution. We have however thought it advisable, for the sake of completeness, here to include all the finds which have come to our knowledge in the course of our own investigations and from extant works.

The fungus does not seem to have been found outside Europe, save for a single find recorded from America. There are no recent finds recorded from the Arctic.

America: New Jersey »in cultivated soil« (Ellis l. c.).

Norway: Oslo; L. Elvedal.

Sweden: Småland (EL. FRIES 1825); »his in terris copiosissimum in humo fagetorum »(EL. FRIES 1829); Svealand (EL. FRIES 1846).

Denmark: Generally distributed, see below under Ecology.

England: Hampstead (SOWERBY 1800; locus classicus!); in crusts of *Lecidea uliginosa* (sec. FRIES 1829); »in woods where the soil is peaty, common« (BERKELEY 1860).

Belgium: Properly determined specimens are found in the following exsiccata: LIBERT, Plantæ cryptogam. Arduenn. No. 181; DESMAZIÈRES: Plantes cryptogam. de France No. 1021; WESTENDORP & WALLAYS: Herbier cryptogam. Belge No. 79.

France: Near the Pyrenees (DUFOUR sec. FRIES 1825); Bruyères (MOUGEOT sec. FRIES 1829); very common in woods near Paris (TULASNE 1862); Poitiers (LACROIX sec. TULASNE 1862).

Germany: Fairly frequent in beech woods in Thuringen (WALLROTH 1833); in foliage woods and dry bogs; »Reichenberg in Böhmen« (CORDA 1839); very common in woods (SCHMITZ 1843); Oestricher Wald (FUCKEL 1869); generally distributed in North and Middle Germany (C. A. WEBER in litt.).

Russia: South-west Russia (WEINMANN 1834).

Italy: Oak and chestnut woods near Milan (VITTADINI 1843).

5. ECOLOGY.

Our researches, covering many years, as to the manner of occurrence of *Cenococcum graniforme* in this country have shown that the species is a typical plant of the »mor« soil. It is found sometimes in woods, sometimes on heaths and in bogs; and under greatly varying conditions as regards moisture; it can grow both in wet *Sphagnum* tufts and in the driest *Lecidea* mor on high *Calluna* heaths. — Sometimes, the sclerotia are found lying above the naked mor soil, but as a rule they are found embedded in the upper layer of mor, being especially common in the rhizoid felt of the mosses, or just beneath it. We give in the following an ecological survey of the conditions, each locality being dealt with separately; where previous writers have furnished any contribution to the ecology of the fungus, the point is noted under the proper heading.

Beech woods.

In beech mor, *Cenococcum* is often found in particularly great numbers; it is met with where the mor layer is well developed and also where it is only thin; even, indeed, in places with »black sand.« In true mould, however, we have never succeeded in finding it. It follows the mossy soil for preference, but may also be found under phanerogamous plants and on spots devoid of vegetation.

Astrophyllum hornum. We rarely failed to find *Cenococcum* under this moss. We have on numerous occasions demonstrated the occurrence of the species here, both in Jutland and Sealand; e. g. on mor slopes near Aarhus and in the woods of North Sealand.

Dicranum scoparium. Beneath this moss also, which often occurs together with the foregoing, *Cenococcum* may be found in abundance (N. Sealand: Ørholm, Frederiksdal; in the latter locality we found the sclerotia situated directly under the green, vegetating parts of the moss stalk, at the tip of the uppermost leaves from the previous year).

Stereodon cupressiformis. At Færgelunden, N. Sealand, we have noted the fungus under this moss, in sandy rather thin »mor« in beech woods; in Marselisborg woods, near Aarhus, we found Cenococcum growing under a small solitary tuft of *Stereodon* in *Anemone-Oxalis* formation (On *Calluna*-heaths, where the allied *Stereodon ericetorum* is very common, *Cenococcum* is frequently found together with this species).

Other Mosses. We have occasionally found *Cenococcum* under the following (N. Sealand: Strandmøllen, mor slope in old beech woods): *Astrophyllum undulatum, Hylocomium proliferum* and *Polytrichum juniperinum.* From Mid-Sealand (open, old beech woods near Skjoldnæsholm) *Cenococcum* has been noted from one or two places »under moss between *Deschampsia flexuosa*«, and from the neighbourhood of Aarhus »on gravelly slopes with thin mor, in beech woods, only under mosses«.

Phanerogams. It has been noted above that *Cenococcum* can occur under moss between phanerogamous undergrowth plants in woods *(Anemone-Oxalis, Deschampsia flexuosa)* but the fungus is also capable of thriving on moss-free soil

under herbage. We have found it for instance (N. Sealand: Færgelunden) under *Melampyrum pratense-Deschampsia flexuosa,* in very thin, sandy mor.

Bare mor soil. Here and there, *Cenococcum* may be met with on bare beech mor; near Aarhus for instance we found it between the root toes of beech at a road through a wood, and at Færgelunden, N. Sealand, we found it on bare patches of sand only slightly mixed with mor; these spots were, however, surrounded by moss vegetation (*Astrophyllum hornum* and *Stereodon cupressiformis*). — Here and there throughout the country (at Bøllemosen and Frederiksdal, N. Sealand, and near Silkeborg in Jutland) we have found the fungus in beech mor together with abundant *Elaphomyces granulatus.*

Records from previous writers. E. Fries 1829: Very abundant in beech humus in Sweden.

Wallroth 1833: Fairly common in beech woods in Thuringen.

Schmitz 1843: »Auf und in jeder Hand voll Dammerde, am Grunde von Baumstämmen oder Sträuchern, besonders an Buchen, ist er [*Cenococcum*] in grosser Menge zu finden.«

Gallöe (sec. Th. M. Fries 1909: »I have found it [*Cenococcum*] everywhere (in Denmark) in beech mor, closely enveloped in the peaty mass of the mor; I have found it right up to the surface of the mor, only hidden by an insignificant covering of leaves.«

Lind 1913: In beech woods in the sandy parts of Jutland and Sealand.

C. A. Weber in litt. 1916: »Gegenwärtig scheint *Cenococcum geophilum* in Nord- und Mitteldeutschland nicht selten zu sein. Ich fand die kleinen Fruchtkörper in Heide- und Waldböden, besonders in dem Moder von Eichen-, Buchen- und Fichten (*Picea*) - Wäldern von der Ems bis zur Memel. Ich kann Ihnen die einzelnen Fundorte nicht nennen ausser dem, wo ich die Pflanze zuerst antraf, nämlich bei Hohenwestedt in Holstein, da ich sehr bald glaubte den Eindruck gewonnen zu haben, das *Cenococcum geophilum* bei uns zu den verbreiteten Arten gehört, weshalb ich mir die Einzelvorkommnisse nicht gemerkt habe.«

Oak Woods.

In the old oak woods in the heath tracts of Jutland, *Cenococcum* is evidently generally distributed. We ourselves have only been able to look for it in two such woods, namely Hald Egeskov and Knud Skov. In the former of these, we found *Cenococcum* in *Melampyrum pratense - Deschampsia flexuosa* mor, partly under scattered *Juniperus* and partly under young oaks; in the latter wood we found it under *Hypnum purum* in *Deschampsia-flexuosa* formation.

Records from previous writers. VITTADINI 1843: »In sylvis quercinis (et castaneis) circa Mediolanum, inter muscorum radices hinc inde occurrens. Vere, autumno.«

ROSTRUP 1884: In mor from young oak scrub near Herning.

In Herb. ROSTRUP 1904: Hald Egeskov, in sand under mor.

LIND 1913: By thousands in Querceta in Jutland.

WEBER in litt. 1916: See above under Beech woods, p. 360.

Birch Woods on Peaty Soil.

A locality of this type (Bøllemosen in N. Sealand) was closely investigated by us, *Cenococcum* being found to occur in great abundance in the bog there. This consists partly of high moor with birch woods (the ground flora chiefly *Vaccinium* species and mosses, or bare), partly of adjacent wet *Sphagnum* vegetation. *Cenococcum* was found at this locality in the following plant communities:

1. Dry *Betuletum*, 75—60 cm above winter water level. The sclerotia lay here and there scattered over the bare peat soil in thousands, or were found in quantities under *Vaccinium uliginosum* and *Dicranum scoparium;* here down to 6 cm depth. At one spot, between the root toes of an old birch, the *Cenococcum* balls lay so closely together on the bare peaty ground, (which was interwoven with the mycorrhiza of the birch) that 1/16 sq. m of the surface yielded 172 sclerotia; and even this is by no means the maximum from this locality.

2. Rather moister *Betuletum*, 30 cm above winter water level. Som specimens of *Cenococcum* were found under *Georgia (Tetraphis) pellucida.*

3. *Sphagnetum*, 30 cm over winter water level. Some sclerotia in a tuft of *Sphagnum fimbriatum.*

4. *Sphagneto-Betuletum*, 20 cm over winter water level Som *Cenococcum* balls in a tuft of *Sphagnum fimbriatum*.

5. In a tuft of *Molinia*, 35 cm over winter water level, *Cenococcum* was found among *Dicrana*.

Chestnut Woods.

VITTADINI 1843: »In sylvis [quercinis et] castaneis circa Mediolanum, inter Muscorum radices hinc inde occurrens. Vere, autumno.«

TULASNE 1862: »In castanetis [et ericetis] agri Parisiensis fere ubique, ac quovis anni tempore abundantissime reperitur.«

Common Spruce Woods.

The occurrence of *Cenococcum* in woods of *Picea excelsa* we have only studied in N. Sealand, at the localities noted in the following, all of which lie close together. It appears from our investigations that the fungus can occur both in pure needle mor in very dark spruce woods, and in lighter spots under the green ground vegetation of mosses *(Hylocomium proliferum, Hypnum purum)* and phanerogamous plants *(Deschampsia flexuosa, Vaccinium myrtillus)*.

Our notes as to the separate localities are as follows:

At Kobberdammene: In pure needle mor in very dark spruce woods, not particularly numerous.

In mor of *Hylocomium proliferum-Vaccinium myrtillus*, with some *Deschampsia flexuosa*, in a clearing of the spruce woods.

Near Bagsværd Lake: Under the carpet of *Hypnum purum*, in old, open spruce wood; some *Dechampsia flexuosa* growing through.

At Frederiksdal: Between old stems and leaves of *Hylocomium proliferum*, at the edge of a spruce plantation.

At Hulsø: On a slope in mossy spruce mor.

Records from earlier writers: In herb. ROSTRUP 1905: Stendalgaard plantation (Mid-Jutland) in spruce mould.

LIND 1913: »Under *Picea*, in the sandy parts of Jutland and Sealand«.

WEBER in litt. 1916: See above under Beech woods p. 360.

Mixed Woods.

Records are available from two localities in N. Sealand.

Færgelunden: In the slightly blackish sand under mixed needles and leaves, without moss, in a small grove of larch and silver fir, and of foliage trees, in the beech wood.

Kobberdammene: In the rhizoid felt of a large *Polytrichum* tuft in a clearing with alder and birch in spruce woods.

Heaths.

In the extensive Calluneta in Jutland, *Cenococcum* is of common occurrence. We have found it on many occasions from south to north, under the predominant character plants, *Calluna vulgaris* and *Stereodon ericetorum*, as also in the lichen mor (especially that of *Lecidea uliginosa)* on open spots between tufts of heather. — As regards other heath formations, we have only been able to investigate the lichen heath above the tree line in Norway (Lille Elvedal) where the fungus was also found, though not in great abundance.

Records from previous writers: EL. FRIES 1829: In *Lecidea uliginosa* mor, sent from England.

MOUGEOT sec. FRIES 1829: »In ericetis circa Bryères Galliæ.«

CORDA 1839: In dry bogs.

TULASNE 1862: »In [castanetis et] ericetis agri Parisiensis fere ubique, ac quovis anni tempore abundantissime reperitur.«

FUCKEL 1869: »Auf und in feuchter Haideerde, selten . . . Im Oestricher Wald an mehreren Stellen.«

In herb. Mus. Bot. Hauniensis: Borris Heath (Jutland) in heather mor.

LIND 1913: By thousands in Calluneta in Jutland.

WEBER in litt. 1916: See above under beech woods p. 360.

The investigations recorded in the previous chapter, supplemented by those of earlier writers, enable us to give the following sketch of the ecological conditions for *Cenococcum*.

Cenococcum graniforme is a typical plant of mor soil, its distribution in our continent extending from the chestnut woods of northern Italy to the lichen heaths above the tree-line in Norway. It is especially abundant inter alia in birch bogs and mossy parts of beech woods; but is otherwise able to

thrive under widely dissimilar ecological conditions, in moist, fairly moist or dry surroundings (Beech, oak and chestnut woods; mixed woods, pine woods, heaths and bogs. On bare mor soil; among pine needles and decaying leaves; in tufts of moss, under mosses and lichens; under phanerogamous herbs and dwarf bushes).

Apart from our find already noted above the tree line in Norway, there are, as far as we are aware, no records of the occurrence of *Cenococcum* in alpine regions, nor does it appear to have been recorded from the Arctic. Our knowledge of the palæontology of the species enables us however, to predict almost with certainty the presence of *Cenococcum* both in arctic and in alpine scrub, moor and bog formations; wherever mor is formed, there will presumably be found the requisite growth conditions for this fungus.

6. MORPHOLOGY AND BIOLOGY.

The Mycelium.

The sclerotia of *Cenococcum* are found normally as unattached spherical or roundish bodies in the carpet of vegetation or the upper mor layer, and it is only on microscopical examination that the mycelium of the fungus can be discerned interwoven through the substrate in numerous threads. A particular variety of *Cenococcum*, however, *β. byssisedum* was described as far back as 1829 by EL. FRIES; in this form, the mycelium developes an unusually byssus-like appearance, and is thus very conspicuous:

»*β. byssisedum*, peridiis thallo floccoso late effuso atro insidentibus. — Apud nos ne obsoletissimum quidem fili vestigium, cum in hac var. thallus floccosus valde insignis, peridia ceterum prorsus similia. In Gallia circa Angers. Guepin! (v. s.).«

We ourselves have not, any more than FRIES, encountered this *byssisedum* form in our observations in the field; it is evidently of rare occurrence, or found only under peculiar conditions[1]). The specimens preserved in LIBERT's Pl. Arduenn.

[1]) The material from the first find of *Cenococcum* in Denmark, mentioned by ROSTRUP in 1884, and preserved in the Botanical Museum at Copenhagen, shows that it belongs to the *byssisedum* form. The label states: »*Cenococcum geophilum* FR. Fruits and Mycelium«.

Nr. 181 belong however, to *β. byssisedum,* and on going through these we were able to determine that the byssus in which the *Cenococcum* sclerotia are embedded answers precisely to the normal subterranean mycelium (vide infra). The Byssus is composed of magnificently granulated hyphæ, with a few smooth ones here and there; the diameter of the hyphæ is 5—7 μ, and anastomoses and coremia are frequent.

As the *Cenococcum* sclerotia are often found in enormous quantities in the mor layer, the mycelium of the fungus must also be strikingly frequent in such places. But if this is the case it is hard to imagine that the mycelium should have escaped the notice of mycologists and investigators of the soil. And we find, as a matter of fact, that the mycelium of *Cenococcum* has been described and figured in this country, nearly fifty years back — almost simultaneously with the record of *Cenococcum* itself, though the relation between the two fungus forms was not then realised.

In the first part of P. E. MÜLLER's »Studier over Skovjord« (Studies of forest soil) 1878, E. ROSTRUP deals with some mycelium forms found in beech mor. A mycelium with clamp connections (l. c. Fig. 6) is ascribed to »*Cladosporium humifaciens*« while another, consisting of »brown mycelium threads without clamp connections« (l. c. Fig. 7) is stated as of doubtful systematic position. ROSTRUP's figure of this latter mycelium is reproduced in our accompanying Fig. 4; it consists of two kinds of hyphæ, smooth and granulated; the latter should, ROSTRUP suggests, (l. c. p. 35) be ascribed temporarily to *Sporocybe resinæ* FR.[1]). This brown, granulated mycelium, which is 4—5 μ in diameter, is unquestionably a *Cenococcum* mycelium, and the same applies, it would seem, to the smooth hyphæ, since, as we shall see later on, the mycelium of *Cenococcum* is sometimes granulated, sometimes smooth. As regards the duration of the mycelium, ROSTRUP states that »this microscopic tissue seems to be almost imperishable«.

In the medium in which *Cenococcum* sclerotia are found embedded, we never fail to find the mycelium. The colour and thickness of the hyphæ alter with age; the young hyphæ are yellow, abt. 3 μ diam., the older ones assume first

[1]) Actually stated as »*Sorocybe resinæ* FR.«. But this is a printer's error.

a yellowish brown, later an almost blackish brown colour, and attain a thickness of 4—6 μ. The hyphæ are very often handsomely granulated; not infrequently we find hyphæ which are smooth for part of their length, and then granulated. The granules evidently easily fall away; we may sometimes find a slimy substance with detached granules in. The hyphæ exhibit a marked tendency to anastomose (Fig. 5) and coremium formation; the coremia are composed sometimes of uniform hyphæ, sometimes of mixed forms; we may, for instance, in one and the same coremium, find thin yellow hyphæ and thicker, blackish brown ones; or it may be composed partly of smooth, partly of granulated hyphæ. Another characteristic of the hyphæ is their power of regeneration; from the base of an open hypha element may be formed a new hypha, growing out through the old one. We shall see later on that the actual germination of the sclerotium also proceeds by the intines of the elements growing forth, the newly formed cells emancipating themselves then as hyphæ. The mycelium threads

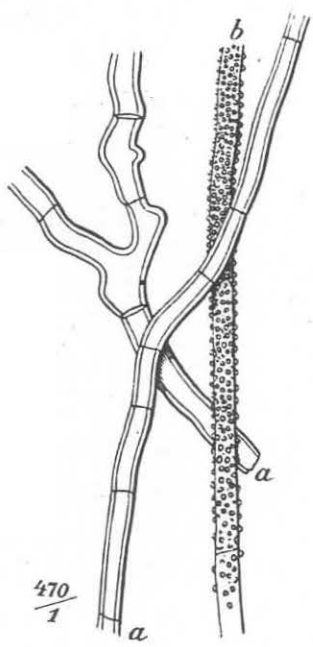

Fig. 4. Copy of Fig. 7, »Brown mycelium threads without clamp connections«, from P. E. MÜLLER'S: Studier over Skovjord (Studies of Forest soil) I.-Belongs to *Cenococcum graniforme*. See Text.

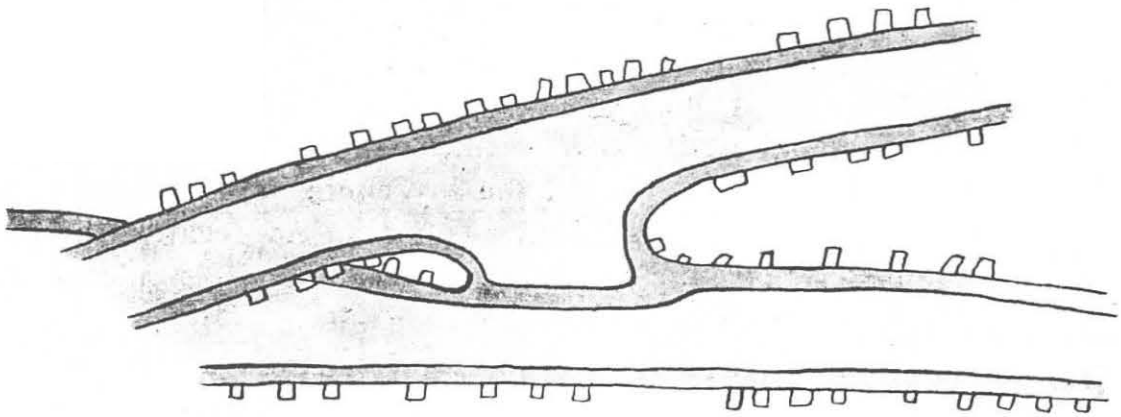

Fig. 5. H-like anastomosing granulated *Cenococcum* hyphæ. × 3000.

can intertwine liana fashion, or twine about moss rhizoids and stems. — It is easy to show, in section, that the hyphæ

described are genetically connected with the *Cenococcum* sclerotium; they are continued directly in the plectenchyme of the bark, the cells of which accordingly have sometimes smooth, sometimes granulated membranes.

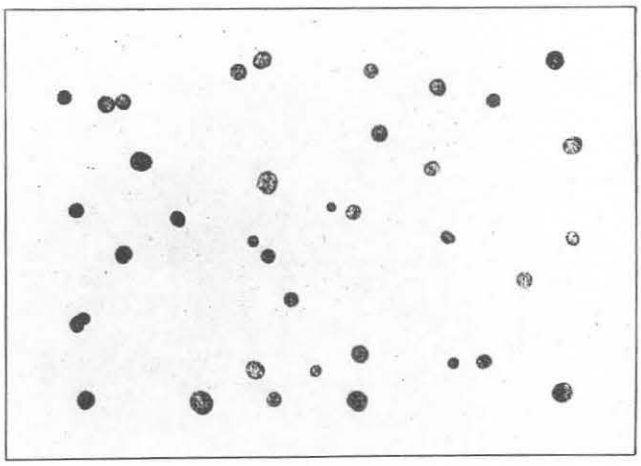

Fig. 6. *Cenococcum* sclerotia from sand under mor. Jutland, Hald Egeskov. Natural size.

The Sclerotium.

The completely formed sclerotia (Figs. 6, 7 and 8) were originally compared by SOWERBY to »small shot« — and the picture is certainly apt enough. When the sclerotia lie out on the bare mor surface, they remind one involuntarily of shot of different sizes, thrown down at hazard. They are black, with a slight sheen, brittle like coal but very hard; as the name implies, they are almost

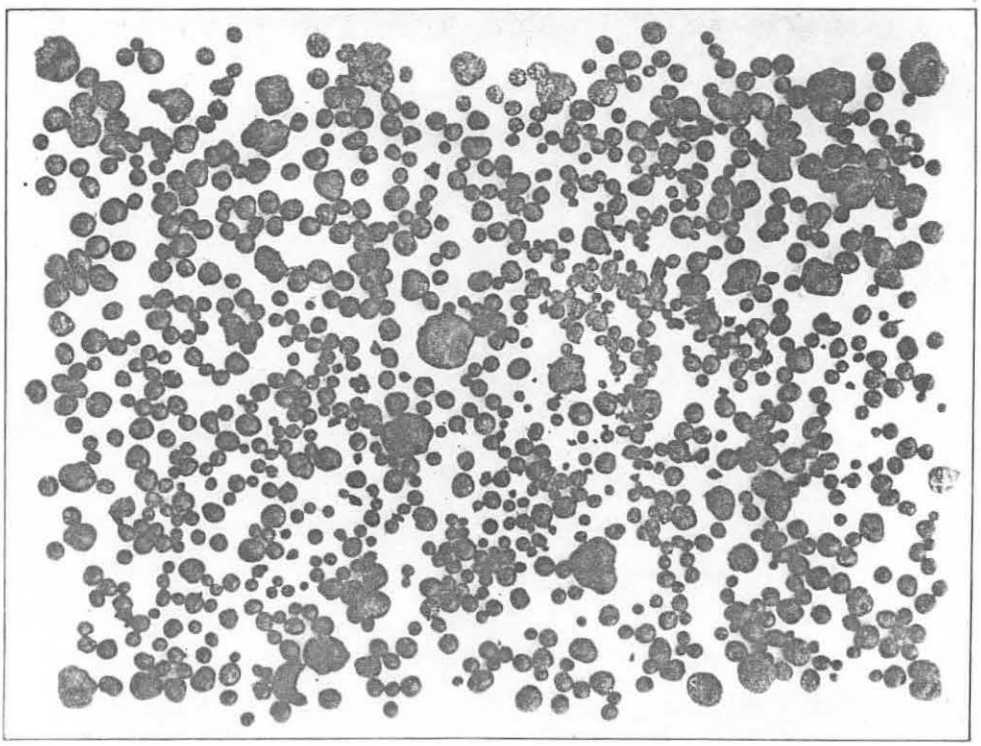

Fig. 7. *Cenococcum* sclerotia from bare peaty soil, near a large birch stump on *Sphagnum* high moor. N. Sealand, Bøllemosen. Natural size.

invariably hollow. The size may vary very considerably even on one and the same spot, and the average differs from one locality to another. In Bøllemosen, N. Sealand, where the sclerotia photographed in the accompanying figures 7 and 8 were taken, we determined the average size of 178 sclerotia, scraped up haphazard from the surface of the soil, and found it to be 2.5 mm[1]); but on the same spot, the size of completely formed sclerotia varies from 0.2 mm to nearly 7 mm. The small and medium sized sclerotia are as a rule spherical,

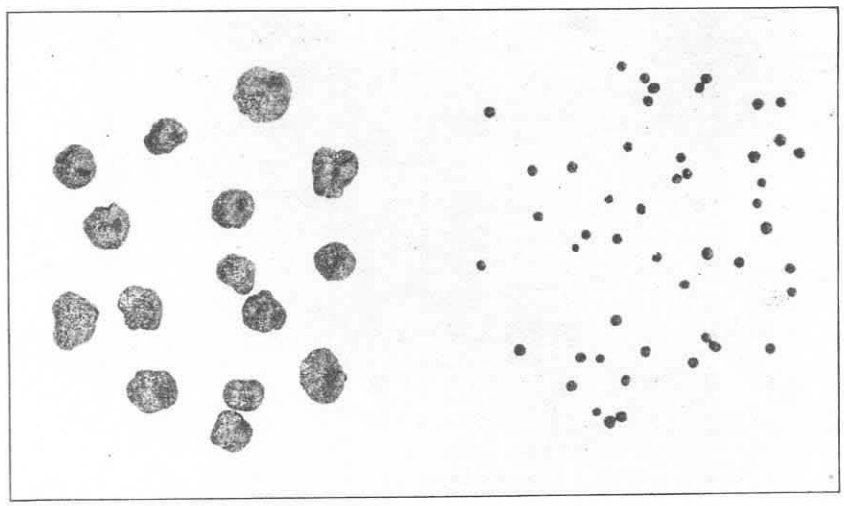

Fig. 8. The largest and the smallest sclerotia from Fig. 7 separately grouped. Natural size.

and roll easily along a smooth surface, the larger ones are irregular lumps (Fig. 8) and often show a distinct point of attachment, like a navel.

As regards the position of the sclerotia, they can, as mentioned, be found lying loose on bare earth; where the soil is mossy, they are most likely to be found in the rhizoid felt of moss or immediately beneath it; deeper down in the mor also, (according to our experience, as far as 6 cm down) they may also be found, while on the other hand they can also be formed right up on the stalks of the moss itself, just under the green vegetating parts.

Corda (1839) who gives the first anatomical contribution to our knowledge of the structure of *Cenococcum*, has already

[1]) The sclerotia from Bøllemosen are on an average over the normal size.

formed a view correct on the whole as to the structure of the sclerotia, and gives a couple of good figures of the same. The transverse sections given by SCHMITZ (1843) and TULASNE (1862) reproduced in Figs. 2 H and 3, must be characterised as excellent, considering the time when they were produced; unfortunately, the interpretation of the figures is in both cases erroneous.

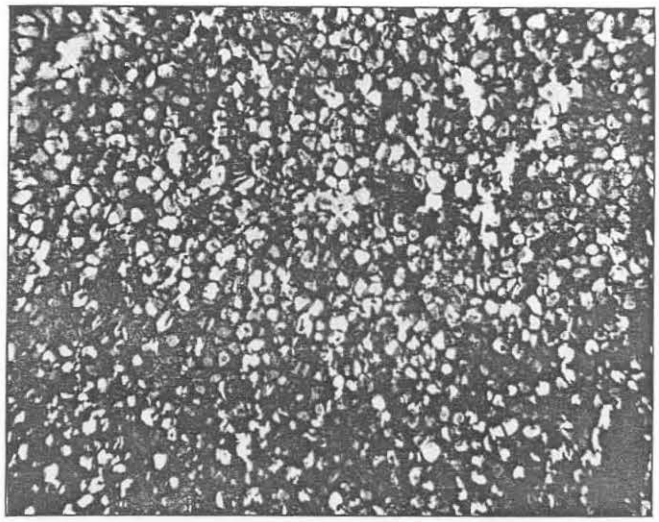

Fig. 9. Part of section of a *Cenococcum* sclerotium. Microphotograph. × 200.

The task of producing a section of the completely formed sclerotium was rendered particularly difficult by the hard and brittle character of the tissue; we succeeded however, in obtaining a continuous microtome section of the sclerotium. The accompanying microphotograph Fig. 9 gives a portion of this section magnified 200 times; Fig. 10 again represents a little part of Fig. 9, magnified 700 times. It will be seen that the interior of the sclerotium consists of an irregular paraplectenchyme; the walls, viewed from the side, appear almost black, in surface view brownish; in accordance with the mode of formation of the sclerotium, they are sometimes single (the original transverse walls) sometimes double (walls which have grown together). The shape of the single element is polygonal; the size varies greatly, the average being somewhere about 10 μ. The section fragment here shown is from the interior of the sclerotium; the bark is smaller-celled, and consists of more elongated elements.

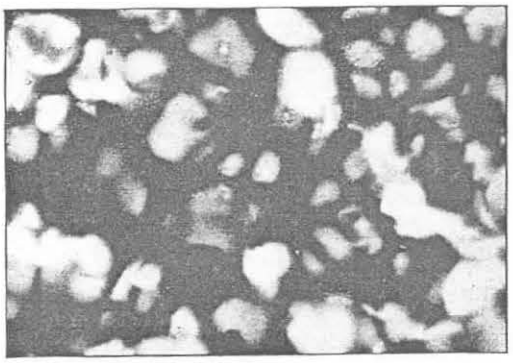

Fig. 10. Detail of Fig. 9. Microphotograph. × 700.

On closer observation of the two section figures it will be seen that many of the cell walls, in surface view, reveal small light coloured, circular spots; these are in reality pores

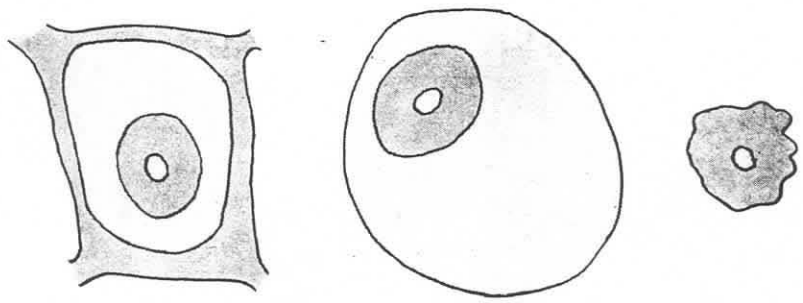

Fig. 11. »TULASNEAN spores« Left: an element of the *Cenococcum* sclerotium with a pore in the wall. Middle: isolated wall with pore. Right: Pore with surrounding roundish and irregular wall-portion has fallen out like a »spore«. × 3000.

in the walls. The precise composition of these pores, whose diameter does not amount to a whole micron, we cannot determine; but their presence is characteristic of the structure of the sclerotium in *Cenococcum,* though they do seem to be lacking in the small-celled bark. A point which greatly helps to render these pores distinct is the fact that the adjacent portion of the wall often assumes a darker colour than the rest of the wall surface and is, moreover, inclined to fall away as a separate roundish, disc-like fragment, with the light pore in its centre. This will be seen from Fig. 11; and it was this which, years ago, lead TULASNE to assume the presence of spores in *Cenococcum* (see Fig. 3 and p. 348). The detached circular or roundish wall fragments with the light-coloured pore may also be very deceptive in their resemblance to spores with an oil globule — and the resemblance is not lessened by the fact that the contour of the »spores« often, as TULASNE rightly observed, appears uneven, as the cell walls of the sclerotium are generally apt to split in zigzag lines. TULASNE's spores, which vary in diameter from $3^1/_2$ to 7 μ, can be found both in light and dark cell

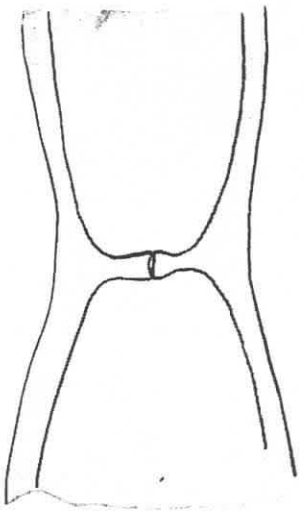

Fig. 12. Optical section at boundary between two hypha-elements; the pore-like connection in transverse wall distinctly visible. × 3000.

walls; in the latter they become in course of time hyaline and indistinct (during the germination of the sclerotium). Fig. 12 shows an optical section at the boundary between two hyphal elements, magnified 3000 times; though the finer structure of the pore is not apparent from this, it is nevertheless evident that a pore-like connection exists between the two cells[1]).

At certain seasons of the year, the *Cenococcum* sclerotium contains great quantities of oil, as already noted by TULASNE; the manner in which this oil content varies with the time of year and the general alteration in the sclerotium in correlation to its phases of development will be described in the following section.

Germination of the Sclerotium.

The first impression which the *Cenococcum* sclerotium produces in the observer is an idea of its unalterable and imperishable nature. These little black balls, brittle and hollow, are in all essentials apparently alike, whether found as last year's growth on a stalk of moss, or imbedded in fresh water strata of interglacial age. But, since the sclerotia, according to the statements of older writers, often contain oil, and since they can occur in tufts of living moss, it is evident that their sub-fossil appearance is not always to be trusted.

Our first endeavours toward solution of the problem tended in the direction of finding sclerotia with abundant oil content, since we considered that such content must indicate approaching germination. Year after year, in the course of our summer excursions, we collected sclerotia in the undergrowth of woods and crushed them between two object glasses in a drop

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1) In the Bot. Zeit. 1892, W. ROTHERT has a series of articles: Ueber *Sclerotium hydrophilum* SACC., einen neuen sporenlosen Pilz. On p. 380 he gives the following description of supposed pores in the transverse walls of the hyphæ; these formations are evidently of similar structure to those of the *Cenococcum,* cf. our Fig. 12:

»Bei Betrachtung mit Immersionssystem und bei guter Beleuchtung sieht man häufig (aber nicht immer) in den Querwänden sowohl dünner als dicker Hyphen drei helle Stellen, die ganz den Eindruck von offenen Poren machen — eine im Centrum und zwei seitlich; dieselben theilen den optischen Querschnitt der Querwand in vier Theile, von denen die beiden mittleren freien etwa doppelt so dick sind als die seitlichen.«

of water; but they always burst like bits of coal, leaving a dry sort of charcoal dust which blackened the water, and under the microscope proved to be composed of small hard, thick-walled plectenchyme elements. As the sclerotia collected at haphazard might naturally be supposed to comprise both dead and living individuals, we continued our investigations, in the hope that we might some day at last succeed in finding a sclerotium containing oil; always, however, without result, as long as we confined our investigations to the dry summer period. We determined then to extend our operations to the winter half year, and this proved to be a step in the right direction. For we found, that the sclerotia collected during the period December—April were in many cases so filled with oil that when crushed in a drop of water between two object glasses, they turned the water milky white with oil emulsion. These sclerotia were not so hard or brittle as the summer forms, and their tissue was found under the microscope to consist of larger and softer elements. The oil exuding turned dark when treated with osmium acid and when suspended in alcohol dissolved completely in chloroform. Among the oil-filled sclerotia we found others in which oil could only be discerned by the aid of the microscope (occasionally as drops along the wall) sometimes, indeed, even the microscope failed, to detect any trace of oil; these last were also found to be hard and brittle.

Our investigations have shown that the *Cenococcum* sclerotium can be filled with oil immediately after the cessation of a period of severe frost; on the 25/2 1917 for instance, on the first day's thaw after six weeks of continual hard frost, abundant oil emulsion was obtained on crushing sclerotia collected from under *Astrophyllum hornum*.

The germination of the sclerotium takes place in conjunction with the mobilisation of the oil, and according to our observations, in the course of winter and spring. The actual process of germination is revealed as follows: The dark cell walls in the interior of the sclerotium (whence the germination proceeds) become more refracting, and begin to jellify and lose colour, the substances contained being presumably resorbed by the cells; the pores in the cell walls become less distinct. A fission of the walls of the elements then takes place, and

the hyaline intines emerge: the newly formed cells are rounded off, 10—16 μ in diameter, and have to begin with highly jellified walls, often with fragments of the burst exines adhering (Fig. 13); the cell-content is no longer homogeneously translucent but granulated-thready or lumpy. After a time the newly formed cells become stretched, and assume a more hypha-like appearance. (Fig. 14).

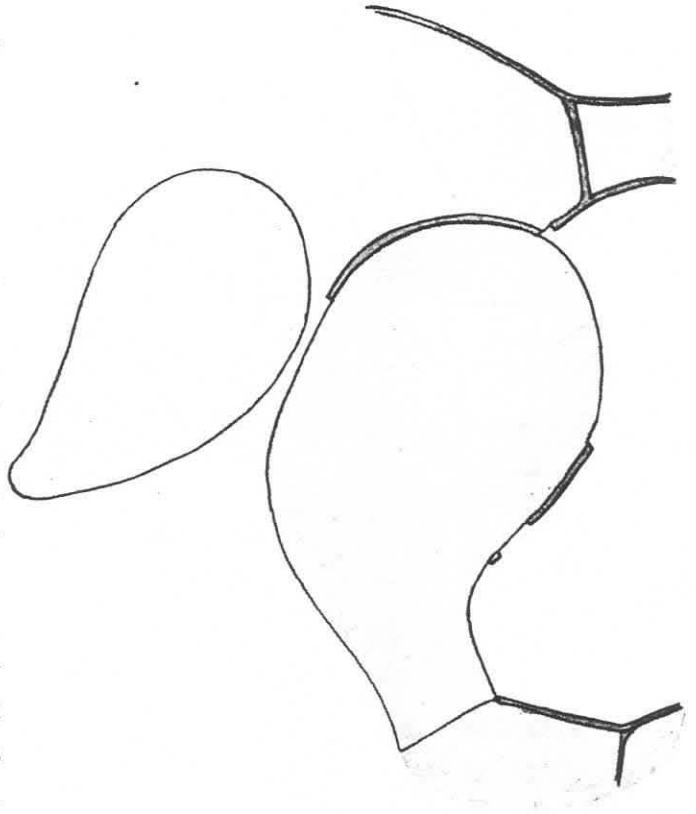

Fig. 13. Germination of *Cenococcum* sclerotium. Portion from the middle of the sclerotium. The elements germinate by cell-renewal, the exines bursting, and the hyaline intines growing out. 14 April. × 3000.

A peculiar phenomenon (divergent germination?) was observed on the 2. April 1916, in the section of a solid *Cenococcum* measuring one millimetre growing under *Astrophyllum hornum* near Aggersø in N. Sealand: most of the elements of the sclerotium are brown, with

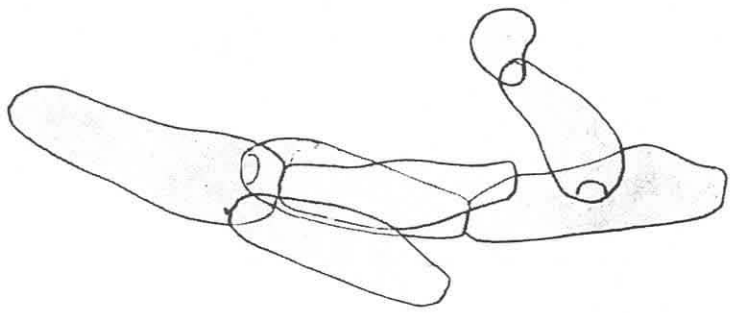

Fig. 14. Farther advanced stage of germination than Fig. 13; the newly formed cells assume a hypha-like appearance. 14 April. × 1000.

distinct pores, and of the usual empty appearance; scattered here and there are elements with a peculiarly coarse-threaded

divided content; this cell content is later liberated in the form of hyaline, gradually yellowing, manycelled spherical or slightly flattened bodies abt. 20 μ in diameter containing the well known oil globules. The complex is somewhat like that of a clathrate spore (Fig. 15).

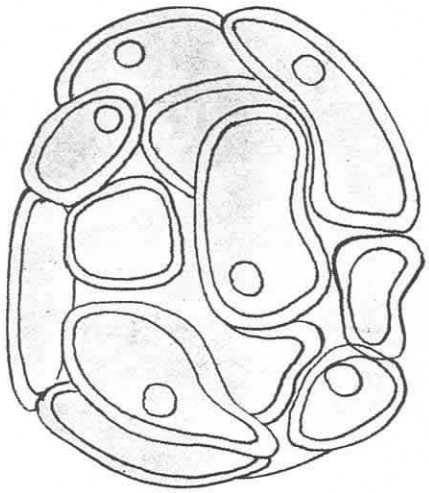

Fig. 15. Isolated cell-complex from germinating *Cenococcum*. See Text. 2 April. × 3000.

Formation of the Sclerotium.

The formation of the *Cenococcum* sclerotium takes place, according to our observations, in the months of June—July, but is difficult to discern, as the young sclerotia are of a brownish colour and therefore easily escape notice in the substrate, which is itself often brownish in colour. With the aid of a binocular microscope however, it may nevertheless be possible to obtain preparations of quite young sclerotia, e. g. from the rhizoid felt of the mosses, where they are formed in great numbers. — In a young state, the sclerotium is light brown, irregularly rounded, somewhat wrinkled and uneven on the outside, and of varying size (in many cases $^1/_2$ mm); it is solid, but soft. The plectenchyme is formed in the usual manner, by swelling and division of the vegetative hyphæ; under the microscope, it appears pale brownish and thin-walled, with homogeneous cell-content. In the earliest stages, the hyphal origin of the tissue is still easily recognisable (as in Fig. 17); after a time however, the inter-

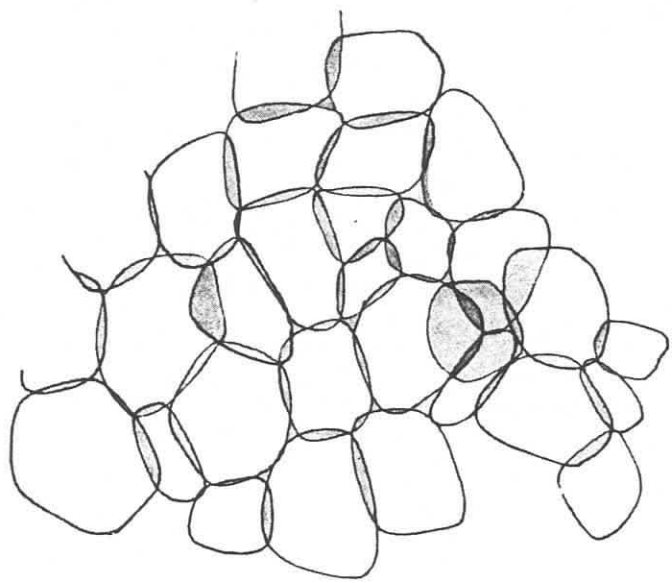

Fig. 16. Formation of *Cenococcum* sclerotium. Thin-walled paraplectenchyme from middle of sclerotium. 5 July. × 800.

cellulars disappear, and a plectenchyme is formed of closely connected cells, which, in the central portion of the sclerotium, are almost isodiametrical (Fig. 16), but towards the periphery elongated (Fig. 17).

Our own investigations of the biology of *Cenococcum graniforme* enable us to state that the hyphæ and sclerotia of this fungus occur in enormous quantities in mor soil in Denmark. The normal cycle of the fungus (which will of course be sub-

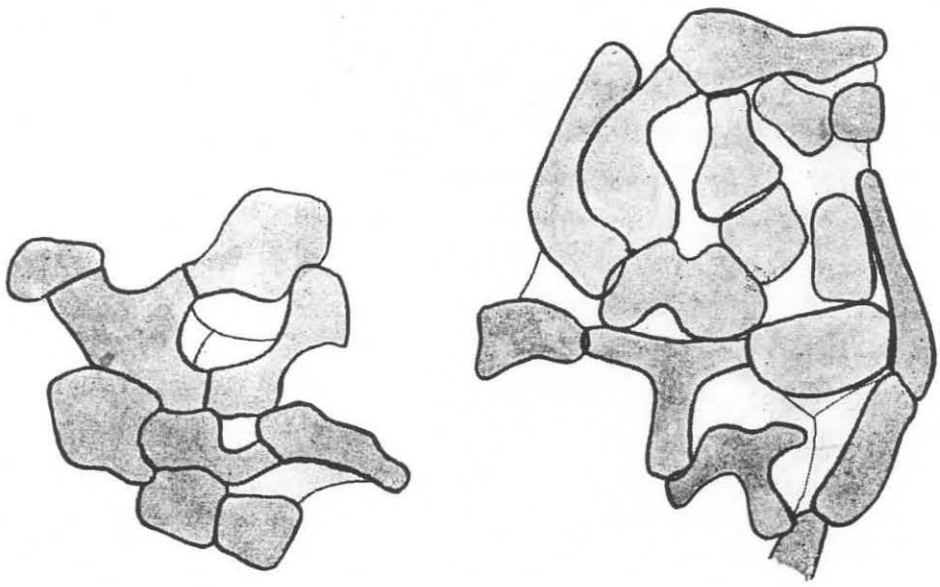

Fig. 17. Formation of *Cenococcum* sclerotium. Plectenchyme from the periphery of the young sclerotium. 1 June. × 1000.

ject to deviation under special conditions) is roughly as follows: The sclerotia are formed in early summer and summer proper, germinating during the period from winter (or late autumn) to spring, when sufficient moisture is available. It may be regarded as altogether improbable that *Cenococcum graniforme* should form any kind of spores or conidia; the species is undoubtedly a *Sclerotium* also in systematic respects, and like several other species (e. g. *Sclerotium hydrophilum* SACC., *S. mucor* TODE and *S. rhizodes* AUERSW.) produces only mycelium and sclerotia. It is obvious that a fungus of so common occurrence must play a considerable part in the transformation of organic material in mor soil.

We have occasionally found dead birch mycorrhiza, up

to a centimetre in length, in the upper mor layer, completely encrusted by the sclerotium tissue of *Cenococcum*, with a black, slightly glistening surface. This suggests the possibility that *Cenococcum*, like many other common earth fungi, occasionally enters into connection also with living tree roots, accessorily in the mycorrhiza sheath or otherwise.

SUMMARY.

In »mor« soil [raw humus] throughout great parts of Europe there are commonly found, embedded in the vegetation carpet or in the upper layer of mor, the small black balls, like shot, brittle like coal, and generally hollow, known in literature under the name of *Cenococcum geophilum*, given them by FRIES. Our knowledge as to the nature of these bodies has hitherto been very incomplete, and the present writers have therefore, throughout a period of several years, made this fungus an object of their studies. These have now shown that *Cenococcum geophilum* FR. is a true sclerotium.

Firstly, as regards its synonymy, (Chap. 1), we have shown, from authentic material, that *Cenococcum geophilum* FR. (1825) is identical with *Lycoperdon graniforme* SOW. (1800), as indeed was also afterwards noted by FRIES himself (1829). The fungus should henceforward be termed *Cenococcum graniforme* (SOW.) COMB. NOV.

In the next section, (Chap. 2) a chronological survey is given of mycological works in which *C. graniforme* is described or figured. Interesting in this connection are especially the works of SCHMITZ (1843) and TULASNE (1862). One of SCHMITZ' illustrations (reproduced in our Fig. 2, D) distinctly shows that this writer discovered the clamp connections in the Basidiomycetæ — though he himself was unaware of the fact, inasmuch as he was looking for the first development stages of *Cenococcum* — 13 years before HOFFMANN (1856) to whom the discovery of these clamp connections is generally attributed. SCHMITZ' work however, is full of erroneous interpretations; the oil globules found in the elements of the scle-

rotium for instance, are described by him as spores. TULASNE corrects SCHMITZ' errors and gives an excellent description and figure of the structure of the sclerotium; the spores which TULASNE indicates however, are likewise unable to stand the test of closer examination, being in reality wall fragments with a fairly regular roundish outline, cut out round a pore in the wall (see Figs. 3 and 11).

Altogether, the various literary documents here brought forward show very distinctly that only the older writers have made any serious attempt to ascertain the true nature of *Cenococcum*. The culmination is reached by TULASNE 1862. Recent writers have not concerned themselves with anatomical investigation of the fungus; they offer nothing new beyond contributions to its ecology, and even here their ideas gradually become uncertain and erroneous. It seems as if the botanists had »given up« this fungus. During the present century, it has even been suggested that *Cenococcum* possibly does not belong to the recent fungus flora; it has been doubted indeed whether *Cenococcum* is a true fungus at all.

In Chapter 3 we have set forth the most important statements in the literature as to the palæontology of *Cenococcum graniforme*. The *Cenococcum* sclerotium is a fossil of frequent occurrence in fresh water deposits of widely varying character, from pleistocene to subrecent times. The first palæontologist to call attention to the fossil occurrence of *Cenococcum* was C. A. WEBER (1896). We have been able to examine fossil specimens of *Cenococcum* from two different places, interglacial and subrecent respectively. The sclerotia were, in point of habitus and microscopically, altogether alike, resembling also in all essentials dry recent sclerotia (having, for instance, distinct »TULASNEAN spores«). The wall colour of the paraplectenchyme (surface view) however, was a shade deeper reddish brown in the fossil specimens than in living forms.

Chapter 4 deals with the geographical distribution of the fungus. From fossil and recent finds of sclerotia it may be assumed that *Cenococcum graniforme* is to this day commonly to be found in ecologically suitable localities in the arctic and temperate zones of the northern hemisphere. Finds are recorded in the literature from the U. S. A., Norway, Swe-

den, Denmark, England, Belgium, France, Germany, Russia and Italy.

The investigations dealt with in Chapter 5, together with the statements of previous writers, enable us to give the following outline of the ecological conditions: *Cenococcum graniforme* is a typical mor plant, its distribution in our continent extending from the chestnut woods of northern Italy to the lichen moors above the tree line in Norway. The fungus is especially numerous for instance in birch bogs and in mossy spots in beech woods; it can thrive however, under greatly varying ecological conditions, in moist, semi-moist or dry surroundings (beech, oak, chestnut woods; mixed woods, pine woods, moors and bogs; on bare mor soil; among pine needles and decaying leaves; in tufts of moss; under mosses and lichens; under phanerogamous herbs and dwarf bushes).

Apart from our find above recorded, beyond the tree line in Norway, there are, so far as we are aware, no records of the occurrence of *Cenococcum* in alpine tracts, nor does it appear to have been noted from the Arctic. Our knowledge of the palæontology of the species however, enables to predict almost with certainty that it will be found both in arctic and alpine scrub, moor and bog formations; wherever there is any formation of mor there will presumably be the requisite conditions for the growth of this fungus.

Chapter 6 treats of the morphology and biology of *Cenococcum*. Our own investigations enable us to assert that the hyphæ and sclerotia of the fungus occur in enormous quantities in mor soil in Denmark. The normal cycle of the fungus (subject of course to deviation under exceptional conditions) is roughly as follows: The sclerotia are formed in early summer and summer proper, germinating during the period from (late autumn or) winter to spring, when sufficient moisture is present. The mycelium is yellow to blackish brown, according to age, sometimes smooth, sometimes handsomely granulated, 4—6 μ diameter; it has been figured by ROSTRUP (in P. E. MÜLLER l. c.) as far back as 1879 (Fig. 4) and was temporarily ascribed by him to *Sporocybe resinæ* FR.

The sclerotium in a young state is light brown, irregularly rounded, somewhat wrinkled and uneven on the outside, varying in size (in many cases $^1/_2$ mm); it is solid,

but soft. The plectenchyme is formed in the usual manner, by swelling and division of the vegetative hyphæ; under the microscope, it appears pale brownish and thin-walled, with homogeneous cell content. In the first stages, the hyphal origin of the tissue is still easily recognisable (as in Fig. 17); gradually, however, the intercellulars disappear, and a plectenchyme is formed of closely connecting cells, which in the middle portion of the sclerotium are almost isodiametrical (Fig. 16) but more elongated towards the periphery (Fig. 17).

The fully formed sclerotium is black, slightly glistening, brittle like coal, but very hard, and generally hollow. The size may vary very considerably in a single locality (from $^1/_5$ mm to nearly 7 mm), and the average size varies from one locality to another. The small and medium sized sclerotia are as a rule spherical, and roll easily along a smooth surface; the large ones are irregular lumps (Fig. 6, 7 and 8). Figs. 9 and 10 show sections of the thick-walled, dark paraplectenchyme of the sclerotium; in the cell walls (surface view) some small, light, circular spots appear, which are in reality pores in the walls. Fig. 11 shows that the pore may be surrounded by a darker roundish section of the wall, which is apt to fall away from the rest, and the fragments thus isolated may resemble spores with an oil globule, — TULASNE indeed regarded them as such (cf. Fig. 3). Fig. 12 shows an optical section through a pore.

The germination of the sclerotium commences by the filling of the cells with oil, often to such a degree that the sclerotium, when crushed in a drop of water between two object glasses, turns the water milky white with oil emulsion. The actual germination process makes itself apparent as follows: The dark cell walls in the interior of the sclerotium (whence germination proceeds) become more refracting, and begin to jellify and lose colour, the contents presumably being resorbed by the cells; the pores in the cell walls become less distinct. The walls of the elements then split, and the hyaline intines appear; the newly formed cells are rounded, 10—16 μ in diameter, the walls at first highly jellified, often with fragments of the burst exine adhering (Fig 13). The newly formed cells stretch in course of time and assume a more hypha-like appearance. (Fig. 14).

It may be taken as altogether improbable that *Cenococcum graniforme* should form any kind of spores or conidia; the species is undoubtedly a *Sclerotium*, also in systematic respects, and like several other species (as for instance *Sclerotium hydrophilum* SACC., *S. mucor* TODE, *S. rhizodes* AWD.) only produces mycelium and sclerotia. — It is clear that a fungus of so common occurrence must play a considerable part in the transformation of organic material in mor soil.

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